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Differential Spring Migration in the White-throated Sparrow (*Zonotrichia albicollis*)

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Abstract

Differential migration timing between distinct classes of individuals is commonly observed in songbirds, however, the underlying behavioural mechanisms of differential timing are still uncertain for most species. My research applied a suite of advanced techniques to examine differential migration timing (between the sexes and between the genetically distinct white-striped and tan-striped morphs) and its underlying behavioural mechanisms (refuelling rate, stopover duration, and wintering latitude) in spring migrating White-throated Sparrows (*Zonotrichia albicollis*) at a key stopover site. Protandry was the only form of differential migration timing observed, with males arriving at stopover on average 11 days earlier than females. Males and females had similar refuelling rates, stopover durations, and wintering latitudes, and morph did not influence any migratory behaviours examined. This study adds to the mounting evidence that differential migration timing does not result from differences in stopover behaviour.

Keywords

Avian, Migration, White-throated Sparrow, Stopover, Refuelling, Wintering Latitude, Stopover duration, Behaviour, Mechanism, Body condition, Spring, Stable isotopes, Plumage morph, Protandry

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Co-Authorship Statement

All work presented in this thesis was completed under the supervision of Dr. Yolanda E. Morbey and Dr. Christopher G. Guglielmo at the University of Western Ontario. All work was done in collaboration with Dr. Yolanda E. Morbey and Dr. Christopher G.Guglielmo, who helped develop the study objectives and methodology. Data collection and analysis was completed by Andrew T. Beauchamp. This thesis has been written by Andrew T. Beauchamp and will be published with Yolanda E. Morbey and Christopher G. Guglielmo.

List of Tables

List of Figures

List of Appendices

List of Abbreviations

ADP - adenosine-5’-diphosphate

AFAR - Advanced Facility for Avian Research

ANOVA - Analysis of variance

ASY - After second year (Adult)

ATP - adenosine-5’-triphosphate

CV - Coefficient of variation

DNA - Deoxyribonucleic acid

dNTP - Deoxynucleoside triphosphate

EDTA - Ethylenediaminetetraacetic acid

EPC - Extra-pair copulation

ESPA - sodium N-ethyl-N-(3-sulfopropyl) m-anisidine

G-1-P - glycerol-1-phosphate

GIS - Global information system

GK - glycerol kinase

GPO - glycerol phosphate oxidase

GPS - Global positioning system

INT - iodonitrotetrazolium chloride

LPBO - Long Point Bird Observatory

LSIS - Laboratory for Stable Isotope Science

NAD - nicotinamideadenine dinucleotide

PC - Principal component

PCA - Principal component analysis

PCR - Polymerase chain reaction

POD - Peroxidase

QMR - Quantitative magnetic resonance

RFLP - Restriction fragment length polymorphism

RI - Refuelling index

SD - Standard deviation

SDS - Sodium-dodecyl-sulfate

SE - Standard error

SY - Second year

TC-EA - Temperature conversion – elemental analyser

TNES - TRIS-NaCl-EDTA-SDS

TRIS - Trisaminomethane

VSMOW - Vienna standard mean ocean water

δ^2H – Stable hydrogen isotope

δ^2H_f - Feather stable hydrogen isotope

δ^2H_p- Precipitation stable hydrogen isotope

4-AAP - 4-aminoantipyrine

Introduction

Animal migration is a fascinating ecological phenomenon, involving all biological levels of organisation from genetic to population (Dingle and Drake 2007). The complexity of migration is mirrored only by its ubiquity across taxa, occurring in a wide diversity of animals from Monarch Butterflies (*Danaus plexippus*) (Urquhart and Urquhart 1978) to Humpback Whales (*Megaptera novaeangliae*) (Rasmussen et al. 2007). Migration is a specialised type of movement that takes an animal away from its immediate home range, usually as a pre-emptive response to local resource decline. Specialised behavioural and physiological adaptations are often exhibited in relation to the triggering, commencement, energy allocation during, and cessation of migration (Dingle 2014). The expression of these attributes can vary across taxa, between species, and within a species between individuals, resulting in substantial diversity in migratory behaviours across the animal kingdom. Likely the most familiar form of migration is to-and-fro migration between two discrete locations, as exhibited by numerous vertebrate species. However, migration can also occur as a loop between several sites (Willemoes et al. 2014) or as a series of one-way trips undertaken by multiple generations, as in the Monarch Butterfly and Painted Lady Butterfly (*Vanessa cardui*) (Urquhart and Urquhart 1978, Stefanescu et al. 2013).

Temporal and spatial heterogeneity in resource abundance and environmental conditions likely drives the evolution of migration as a life history strategy to maximise survival and reproductive success (Dingle 2014). Selective pressures imposed by the environment that migratory animals inhabit has shaped the evolution of behavioral, physiological, morphological, and other life history traits that control individual migration (Dingle 2006, Dingle and Drake 2007, Åkesson and Hedenström 2007). In the era of global climate change, predicting how migratory animals will adapt to changes in the environment is fundamental to forecasting the consequences of the coming change on migratory species. This will require a thorough understanding of migration through all biological levels of organisation (from the underlying genome to the resultant population level movement patterns), how these levels interact with the environment, and the interrelation between migration and other critical life history events. The diverse variety

of migration exhibited in birds provides an excellent model system to study migration at all organisational levels. Additionally, multiple studies have shown that migratory avian populations are already responding to climate change (Visser et al. 1998, 2004; Root et al. 2003, Both et al. 2006, Hedenström et al. 2007, Charmantier et al. 2008). By studying avian migration, we can both develop our understanding of animal migration and provide information to help predict how avian populations may respond to a changing environment.

In this introduction, I will briefly introduce avian migration, covering some of the behavioural aspects of North American bird migration leading to the phenomenon of differential migration timing. After summarising the leading hypotheses for why differential migration occurs, I will explain three key behavioural mechanisms believed to result in differential migration timing and how these mechanisms can be studied in free living songbirds. I will then introduce the focal species of this study, and what is known about differential migration in this species, before moving into specific hypotheses and predictions.

1.1 Avian migration

The seasonal migration of birds is a spectacular phenomenon that is estimated to involve over 50 billion birds around the globe (Berthold 2001). Migration is a behaviour exhibited by nearly 2000 species across a diverse variety of avian taxa (Birdlife International 2018). Many migratory bird species exhibit the classic to-and-fro migration pattern, travelling thousands of kilometers between temperate breeding grounds and tropical overwintering areas during alternate times of the year (Dingle 2014). Temperate avian communities are largely composed of migratory species (Newton and Dale 1996), of which a substantial number are songbirds (order Passeriformes). These small-bodied birds often migrate thousands of kilometers each way during migratory seasons. In North America, many species migrate from temperate breeding areas in boreal Canada to overwintering areas in Central and South America. To accomplish these often-lengthy journeys, migratory songbirds exhibit many specialised behavioural and physiological adaptations. Many North American songbird species shift from a primarily diurnal activity pattern, to a pattern of diurnal foraging and nocturnal migratory flight. This

behaviour allows migrants to maximise daylight foraging, but may also be related to favourable flight conditions and nocturnal orientation cues (Alerstam 2009). The body shape, wing shape, and skull size of migratory bird species often differs compared to similar non-migratory species (Winkler and Leisler 2005, Dingle 2014). Body composition and organ size can also change during migration (Guglielmo and Williams 2003), likely as an adaptation to reduce flight costs (Piersma 1998). Most migratory birds also increase food intake, becoming hyperphagic prior to and during migratory periods (King and Farner 1965). Fat is the primary fuel of migration, and migratory songbirds exhibit a number of adaptations which result in extreme proficiency in both the storage and use of fat (Guglielmo 2018). Despite possessing a complex suite of adaptations, most migratory species do not complete migration in a single flight, often requiring multiple stops to rest and replenish depleted energy stores during the course of migration. Somewhat counterintuitively, evidence suggests that a greater proportion of time and energy are spent at stopover locations during the course of migration (Hedenström and Alerstam 1997, Alerstam and Hedenström 1998, Wikelski et al. 2003), indicating that birds spend less time flying than in other activities over the course of migration. Migration is also hazardous, and birds face a number of elevated risks during migration, including: predation, disease, exhaustion, starvation, and inclement weather (Newton 2008). These risks likely contribute to the elevated mortality rate associated with the migratory period (Sillett and Holmes 2002, Klaassen et al. 2013, Lok et al. 2015).

Evidence suggests that many songbirds migrate following a strategy aimed at reducing the amount of time spent in migration (Lindström and Alerstam 1992, Hedenström 2008). Minimising the time spent during migration may be beneficial for a variety reasons. Migration can constitute a large portion of a birds' annual life cycle, and reducing the time spent migrating may provide more time for other life cycle stages. For birds breeding in temperate areas, reproductive activities (display, courtship, nest-building, incubation, raising young to independence) and moult must be completed in the limited time during which breeding area conditions are favourable (McNamara et al. 1998). Faster migration may also minimise the time spent in hazardous unfamiliar territory, acting to reduce the risks. Migration speed may also be a limiting factor in total migration distance after accounting for the time required for reproduction and other

behaviours such as moult. A faster migration speed may enable birds to exploit suitable habitat greater distances away from overwintering areas. Finally, faster migration may enable earlier arrival at breeding areas. Migration must be completed before reproduction and being present at breeding areas at an earlier date may allow for the synchronisation of reproduction to early season peaks in resource abundances thereby resulting in increased individual fitness (Perrins 1970, Smith and Moore 2005). Additionally, earlier nesting may improve offspring condition and post-fledging survival (Mitchell et al. 2011).

As periodic stopover bouts are required over the course of migration, the optimal strategy to minimise migration time must consider both the flight speed and the time spent in migratory stopover. The relationship between lift, drag, weight, and flight costs results in diminishing returns on potential flight range gained for each additional unit of fat added, allowing for predictions to be made about optimal departure fuel load, stopover duration, and flight speed in response to the pressure to minimise total migration time (Alerstam and Lindström 1990). The departure fuel load under a time minimisation strategy is expected to relate positively to refuelling rate, with migrants departing from stopover with a higher fuel load when refuelling rates at that location are high. Variation in refuelling rate could potentially result from extrinsic factors such as site quality (Lindström and Alerstam 1992), or from intrinsic differences in individual refuelling ability (Heise and Moore 2003). Time motivated migrants are expected to depart from stopover when the marginal rate of gain in potential flight distance drops to the expected average speed of movement for the entire migratory journey (Alerstam and Lindström 1990). The negative relationship between fat mass and potential flight distance suggests that birds with greater fat mass (whose gain in potential flight distance is low due to high transport costs) should continue migration, rather than remain at a stopover site to forage while only increasing potential flight range marginally. Together, this relationship suggests that the duration of stopover for time-selected migrants should depend on the rate of fuel deposition. Theoretically, rapid refuelling will result in a faster decrease in the potential flight distance gained for each unit of fuel added, resulting in shorter optimum stopover durations when refuelling rate is high (Alerstam and Lindström 1990).

Besides refuelling rate, wind assistance may alter departure fuel load and stopover duration. With a tailwind, migrants may advantageously depart from stopover earlier and with lower fuel loads than under calm conditions (Weber et al. 1998). The amount of time spent in non-fuelling stopover behaviours could also influence the duration of stopover. Time spent searching for food, settling in a suitable patch, or regenerating digestive organs adds to the total duration of stopover, with longer settling times resulting in a longer stopover duration. Finally, flight speed under a time minimisation strategy should also be higher than flight speed under an energy minimisation strategy (Alerstam and Lindström 1990).

1.2 Differential migration in an avian context

In many songbird species, different sex and age classes will migrate on different time schedules or overwinter at different locations. This phenomenon, known as differential migration, can formally be defined as "the situation in which migration in some distinguishable classes of individuals (ages, sexes, races) differs with respect to timing, distance, or both" (Terrill and Able 1988). Differential migration timing is found in many songbird species, often occurring between sexes with males and females migrating on different schedules (Oring and Lank 1982, Francis and Cooke 1986, Reynolds et al. 1986, Morbey et al. 2012). Protandry, where males arrive before females at all locations up to- and including the breeding sites, has been reported numerous times in multiple migratory bird species (Francis and Cooke 1986, Morbey and Ydenberg 2001 and references therein, Kissner et al. 2003, Rubolini et al. 2004, Morbey et al. 2012 and references therein). In a review of eight comparative studies, Morbey et al. (2012) found evidence of migratory protandry in 71 species, with males preceding females by an average of 5.2 days. Protogyny, where females precede males, occurs less frequently but is exhibited in several bird species with reversed sex-roles, such as the Spotted Sandpiper (*Actitis macularius*) (Oring and Lank 1982, Reynolds et al. 1986). Differential migration timing can also occur between age classes. In general, it is more common for older birds to migrate to breeding sites earlier than younger birds (Francis and Cooke 1986, Lozano et al. 1996, Stewart et al. 2002, McKinnon et al. 2014). For example, adult male American

Redstarts (*Setophaga ruticilla*) arrive at migratory stopover areas and breeding areas well in advance of younger males in the spring (Lozano et al. 1996, Stewart et al. 2002).

The ecological and evolutionary implications of differential migration are far reaching for migratory bird species. The timing of migration can affect the environmental and ecological conditions encountered during migration and can affect the costs associated with migration (Wikelski et al. 2003, Robson and Barriocanal 2008, Klaassen et al. 2013, Lok et al. 2015). For example, early spring migrants may be more likely to encounter inclement weather conditions, which can result in decreased body condition (Robson and Barriocanal 2008). Severe weather events can even result in mortality among early season migrants (Whitmore et al. 1977, Møller 1994). Therefore, there must be benefits associated with earlier arrival that differ between individuals.

1.3 Hypotheses for differential migration

Multiple non-mutually exclusive hypotheses have been posited regarding the adaptive significance of sex-specific differential migration timing. These hypotheses are often framed in regard to protandry, however, most can also be applied to birds with sex-role reversed mating systems. Competition between males for high quality territory was previously believed to be a major driver behind the evolution of protandry. Termed the 'rank advantage hypothesis', earlier arriving males were thought to receive a 'rank advantage' in the competition to secure a high-quality breeding territory. Owners of a high quality territory then received 'priority benefits' associated with high quality territory (Kokko 1999, Morbey and Ydenberg 2001). Prior occupancy is advantageous during competition for territory (Krebs 1982, Tobias 1997), suggesting that earlier arrival aids in territory acquisition and retention. Additionally, later arriving birds can be in poorer condition (Møller et al. 2009), which may reduce the ability of later arriving birds to supplant earlier arriving territory owners (Nyström 1997).

While initially popular, the rank advantage hypothesis has drawn criticism because reproduction in a high-quality territory can provide fitness advantages for both sexes. Competition between females for males occupying high quality territories could also select for earlier migration by females, reducing the degree of protandry exhibited in

a population. Developing the rank advantage hypothesis further, the "mate opportunity hypothesis" considers why males should arrive earlier *relative* to females (Morbey and Ydenberg 2001, Kokko et al. 2006). By being present at breeding sites prior to the arrival of females, males have more opportunities to mate with early arriving high quality females, and have the potential to mate with other partners outside of their social pairing as the season progresses. For example, Reudink et al. (2009) found that earlier arriving American Redstarts achieved greater polygyny, siring more extra-pair offspring than later arriving birds. Møller et al. (2009) found that earlier arriving male Barn Swallows (*Hirundo rustica*) sired more offspring and had less extra-pair offspring in their nest compared to later arriving males. In addition, pairs formed of later arriving males and earlier arriving females (i.e., a lower degree of protandry within the pair) had more extra-pair offspring in their nests, providing additional selection pressure for earlier male arrival. Other benefits, such as a reduction in mate acquisition time, earlier clutch initiation (Rowe et al. 1994), and increased time available to re-nest (Townsend et al. 2013) can provide further benefits associated with earlier arrival relative to females (Kokko et al. 2006).

Other hypotheses for differential migration timing include the 'susceptibility' and 'constraint' hypotheses. Under the susceptibility hypothesis, protandry occurs because larger males, which are generally larger than females, are better able to tolerate adverse weather conditions, allowing for earlier migration (Morbey and Ydenberg 2001). In both the rank advantage and mate opportunity hypothesis, the cost of early migration can manifest through exposure to inclement environmental conditions (Kokko 1999). Selection may then favour larger male body size in protandrous species (Kissner et al. 2003). The constraint hypothesis states that protandry results from a limitation on migration timing imposed by some other trait. For example, sex-segregation on the wintering grounds may result in differential arrival timing at the breeding grounds if both sexes initiate migration at the same time and migrate at the same speed. The constraint hypothesis is non-adaptive however, and can be confounded by other adaptive hypotheses. For example, selection for protandry may favour males that winter further north when the rate of migration and migration initiation date does not differ between males and female (Morbey and Ydenberg 2001).

The selective pressures driving sex-specific migration may also contribute to age specific migration, taking components from rank advantage, mate opportunity, susceptibility, and constraint hypotheses. In many bird species, juveniles are sub-dominant to adults (Piper and Wiley 1989, Carpenter et al. 1993, Yong et al. 1998, Cristol et al. 1999) and likely have a lower chance of obtaining a territory when competing with adults (Tobias 1997). The reduced benefit of early arrival for less competitive individuals should result in a shift in the optimal arrival time to a later date (Kokko et al. 2006).

Juvenile birds may also face physiological constraints which may increase the cost associated with migration. Juveniles generally have shorter wing spans, which can increase the cost of flight (Åkesson and Hedenström 2007). Juveniles are also less selective of wind while migrating, resulting in reduced migration speed and increased cost per distance flown (Mitchell et al. 2015). More expensive migratory flight likely necessitates the need for frequent refuelling stops (McKinnon et al. 2014), which can further act to constrain juvenile arrival timing. Altogether, the increased cost of migration and reduced benefits of earlier migration may select against early arrival in juveniles, resulting in differential migration timing by age.

1.4 Mechanisms of differential migration timing

To further examine hypotheses regarding the evolution of differential migration timing, additional knowledge is required regarding how individual behaviours result in population level movement patterns. Coppack and Pulido (2009) suggested three main non-mutually exclusive behavioural mechanisms that could underlie differential arrival timing to breeding areas. These are differential migration speed, differential migration distance, and differential initiation timing of migration.

1.4.1 Differential migration speed

Differences in migration speed could promote differential arrival timing to breeding areas. Hypothetically, groups of migratory birds departing for migration from the same

location at the same time could become stratified in their arrival timing if some individuals migrate faster. Migration speed can be affected by the speed of migratory flight, however, the amount of time spent at inter-flight stopover locations likely a greater determinant of overall migration speed (Alerstam and Lindström 1990, Hedenström 2008, McKinnon et al. 2016). Optimal migration theory, supported by some empirical evidence, suggests that individual departure decisions will depend on body condition, and that individuals able to replenish fat stores (refuel) faster will have a shorter stopover and a faster overall migration (Moore and Kerlinger 1987, Alerstam and Lindström 1990, Åkesson and Hedenström 2007, Schaub et al. 2008, Dossman et al. 2016). Group specific stopover refuelling rate may then contribute to differential migration timing. Refuelling performance can vary based on multiple interrelated factors including; predation risk, arrival condition, physiology, local food availability, and competition (Dunn 2000, Schmaljohann and Dierschke 2005, Salewski et al. 2007, Schaub et al. 2008, Seewagen et al. 2013, Smith et al. 2015), but behaviour may also influence refuelling rate. Behavioural traits related to social dominance and competitive ability, often related to sex and age in birds, can provide greater access to food and enable dominant individuals to refuel faster (Caraco 1979, Piper and Wiley 1990, Woodrey and Moore 1997, Yong et al. 1998, Seewagen et al. 2013, Brown et al. 2014). The general dominance hierarchy of males over females, and older over younger often corresponds well to spring stopover and breeding ground arrival timing in many species (Ketterson 1979, Piper and Wiley 1989, Marra 2000, Moore et al. 2003). Despite this, empirical evidence that stopover refuelling performance varies among sex and age classes is still scant and contradictory. Seewagen et al. (2013) found that males had a higher stopover refuelling rate in two protandrous warbler species during spring migration, supporting the notion that males arrive on the breeding grounds earlier through faster refuelling at migratory stopover sites. Other studies have failed to find a similar pattern (Morris et al. 2003, Smith et al. 2015, Morbey et al. 2018). The extent to which sex-specific stopover refuelling rate affects migration timing, and how common this phenomenon is among songbird species, is currently uncertain.

Additional factors may influence the duration of migratory stopover, with potential implications for migration speed. Birds may advantageously depart from

stopover on nights with a tailwind, reducing flight costs through wind assistance and reduced crosswind drift (Sjöberg et al. 2015, Mitchell et al. 2015). Mitchell et al. (2015) found that juvenile Savannah Sparrows (*Passerculus sandwichensis*) were less selective of favourable tailwinds during fall migration, resulting in slower flight speeds and less energetically efficient migration. Air temperature is another environmental variable that may influence migratory stopover duration. Air temperature is known to affect migratory restlessness (a behaviour characterised by extensive movement and correlated to migration patterns of free-living birds) in birds (Metcalfe et al. 2013), and may act as an environmental cue encouraging departure from stopover. Additionally, air temperature may influence stopover duration by affecting thermoregulatory cost (Bowlin et al. 2005). Excessive energy used for thermoregulation during cooler periods may prolong the length of time required to accumulate a sufficient departure fuel load, resulting in delayed departure from stopover. Finally, the frequency of stopover bouts over the course of migration is another factor that could influence overall migration speed. McKinnon et al. (2014) found that juvenile Wood Thrush conducted stopover bouts more frequently during the course of migration, resulting in a slower overall migration speed. Morphological (Yong and Moore 1994, McKinnon et al. 2014) or behavioural (Mitchell et al. 2015) differences between individuals could influence flight energetics, and contribute to differences in the number of stopover bouts required during migration. For example, the advantageous use of tailwind by adult Savannah Sparrows during migration (Mitchell et al. 2015) may enable greater distances to be traversed on a given fuel load (Alerstam and Lindström 1990), reducing the number of stopover bouts required between wintering and breeding areas.

1.4.2 Differential migration distance

Differential migration distance is another behavioural mechanism that can underlie protandry. Hypothetically, if the initiation date and speed of migration are similar for both males and females, overwintering closer to breeding areas would enable males to arrive earlier at breeding areas in the spring. Latitudinal sex segregation on the wintering grounds is known to occur in many bird species, especially in granivores like sparrows and finches (Cristol et al. 1999, Newton 2008). In a survey of literature regarding sex-

based differential migration, Cristol et al. (1999) reported that males wintered closer to breeding areas than females in 41 of 53 species examined. They also identified a further 93 species that likely exhibit differential migration distance, most of which exhibited the typical pattern where males wintered closer to breeding areas. Differences in migration distance could also affect other types of group-specific differential migration timing. Age-specific migration was also reported by Cristol et al. (1999) in 20 of the 53 species identified as differential migrants. In all cases, younger birds migrated a greater distance than adults.

Differential migration distance may result from behavioural or morphological differences between the groups. During the non-breeding season, dominant individuals usually outcompete subordinates for high quality habitat and resources (Piper and Wiley 1989, Choudhury and Black 1991, Marra 2000, Catry et al. 2004). The cost of competition for limited resources at more northerly wintering latitudes could potentially result in subordinate individuals electing to winter further south where resources may be more plentiful. Physical differences between groups may also contribute to differential migration distance. Larger individuals may be better able to tolerate colder conditions at more northern wintering latitudes, allowing for a short migration (Ketterson and Nolan 1976, Jenkins and Cristol 2002).

1.4.3 Differential migration initiation date

Differential initiation timing of migration is another behavioural mechanism that can result in differential migration timing (Coppack and Pulido 2009, Jahn et al. 2013, Schmaljohann et al. 2016, McKinnon et al. 2016). The initiation of migration may be controlled endogenously, or by cues such as photoperiod (Gwinner 1996, Coppack et al. 2008, Maggini and Bairlein 2012). Among protandrous species, captive males have been demonstrated to exhibit nocturnal migratory restlessness at an earlier date compared to females. This pattern holds true when birds are exposed to simulated natural light cycles (Terrill and Berthold 1990) and light regimes of equal length day and night (Coppack and Pulido 2009, Maggini and Bairlein 2012) suggesting that the endogenous circannual mechanisms controlling migration timing differs between males and females. Conditions on the wintering ground can also have carry-over effects on the initiation of migration.

Marra et al. (1998) showed that American Redstarts overwintering in higher quality mangrove habitat initiated vernal migration earlier. In this species, a higher proportion of birds in high quality mangrove habitat were dominant adult males, suggesting that winter habitat selection is mediated partly by behaviour (Marra et al. 1993). Migration initiation can also differ between age classes. Mckinnon et al. (2014) found that juvenile Wood Thrush departed the wintering grounds later than adults. No age-related differences in body mass were found during late winter, suggesting that the differential departure resulted from endogenous programs or age-specific responses to photoperiod.

1.5 Methodological approaches to studying migration

1.5.1 Stopover refuelling rate determination

Past studies have relied on the analysis of morphometric data taken at capture to determine fuel deposition rate. The change in body mass between captures for birds captured multiple times is one method that has been widely employed to estimate stopover fuel deposition rate (Cherry 1982, Yong and Moore 1997, Yong et al. 1998). This method is complicated by the challenge of recapturing individuals, and may be biased by stress resulting from repeated captures and by the increased probability of recapturing low-quality individuals that may remain at stopover sites longer. Regression analysis of single-capture total body mass against time of day is another method that has been used to assess refuelling performance, relying on the general trend that songbirds gain mass during daytime foraging (Winker et al. 1992, Dunn 2000, Wilson et al. 2008). Detecting the relationship between time of day and mass can be difficult however, requiring large sample sizes to control for intraspecific variability in body size that is unrelated to fuel deposition. Plasma metabolite profiling offers a physiological means to obtain an individualistic measure of instantaneous refuelling performance from a single capture (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005, Zajac et al. 2006). Plasma metabolite profiling is based on the physiological principle that the circulating concentration of the blood plasma metabolites triglyceride and β-OH butyrate reflect recent food consumption (Zajac et al. 2006). Triglyceride (triacylglycerol) is an ester composed of three fatty acids bound to a glycerol backbone. During feeding and fat

deposition, plasma triglyceride concentrations rise as lipids are absorbed in the intestines or synthesised in the liver (Jenni-Eiermann and Jenni 1994). β-OH-butyrate (β-hydroxybutyrate, 3-hydroxybutyrate) is a ketone body synthesised by the liver during the catabolism of stored fat. During fasting and fat use, plasma β-OH-butyrate concentration increases as lipids are catabolised (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005). Plasma triglyceride and β-OH-butyrate are negatively correlated, and concentrations can be combined into an index of refuelling (RI) (Guglielmo et al. 2005) useful for exploring questions about stopover physiology and ecology.

1.5.2 Stopover duration determination

As highly mobile animals, tracking migratory birds is a challenging task. Multiple methods are available to track animals, including geographic positioning system (GPS) tags, light level geolocators, and radio transmitter tags (Bridge et al. 2011). In small bodied songbirds, size generally prohibits the use of GPS tags. Most light level geolocators require retrieval, and generally have low spatial resolution. As a result of recent technological advancements, radio telemetry currently offers the best solution to the problems of size, cost, and positional precision for the study of regional scale avian migration ecology.

Radio tags emit a signal that can be detected by a receiver, allowing researches to follow or infer the location of a tagged animal. In the past, individual radio telemetry tags were programmed to emit a simple pulse on a specific frequency. To track multiple individuals, multiple tags emitting pulses at different frequencies were required. This limited the number of tags that could be deployed to the available bandwidths, and required the receiver frequency to be tuned to specific tags. This made it difficult to track large numbers of animals simultaneously. The development of encoded very-high-frequency radio transmitter tags solved this issue. Coded radio tags are designed to emit a unique pulse of radio signals, analogous to an “audio-barcode”. The combination of unique pulses transmitted at known set time intervals allow individual tags to be distinguished while operating on the same frequency (Taylor et al. 2017).

Coded radio tags enabled the development of large-scale automated radio receiver networks, such as the Motus Wildlife Tracking System (henceforth: Motus) (Taylor et al. 2017). Motus is a coordinated array of over 300 automated radio receiver stations located throughout southern Canada and along the east coast of the United States of America. Motus receiver stations generally consist of a tower with one to five nine-element Yagi directional radio antennae affixed to the mast. Under ideal conditions, Motus towers can detect a signal from a radio transmitter over 15 km away, although terrain and weather may influence the detection distance (Taylor et al. 2017). Each time a signal is received from a radio transmitter tag, the transmitter identification number, time, location of receiver tower, antenna number, and signal strength are recorded. The local and regional scale movements of tagged animals can then be tracked by examining the sequence of detections at different receiver stations.

1.5.3 Estimation of migratory origin using stable isotope analysis

Stable hydrogen isotope analysis of feathers and other keratinaceous tissues has been applied by numerous studies to answer questions about migratory connectivity and geographic origins of birds and other migratory animals (Chamberlain et al. 1996, Hobson and Wassenaar 1996, Rubenstein et al. 2002, Bridge et al. 2014, Sullins et al. 2016). The utility of stable hydrogen isotopes (δ^2H) for determining the geographic origin of animals is derived from two main factors: 1) biogeochemical processes create geographic variation in food web isotope signatures, and 2) the isotopic signature of metabolically inert feather tissue reflects the isotopic signature of the local food web where it is formed. Geographic variation in food web isotope signatures results largely from climatic and meteorological processes that effect equilibrium and temperature-related kinetic processes governing the ratio of hydrogen isotopes in precipitation (Taylor 1974). In North America, this results in a general decrease of the stable hydrogen isotope deuterium in precipitation with increasing distance from the equator, creating latitude specific hydrogen isotope signatures (Hobson and Wassenaar 2008). The average local growing-season precipitation hydrogen isotope (δ^2H_p) signature is incorporated through the food chain into the tissues of birds feeding in the area (Yapp and Epstein 1982, Hobson and Wassenaar 1996). During feather moult, dietary δ^2H values are translated

into newly-formed feather tissues (Hobson and Wassenaar 2008). Because feathers are metabolically inert after formation, the feather hydrogen isotopic signature (δ^2H_f) permanently reflects the isotopic signature of the diet of the individual during the feather growth period. These feathers can then act as an intrinsic marker of moulting latitude. For example, some bird species replace body feather on the wintering grounds prior to spring migration. The δ^2H values of the body feather collected at non-wintering sites will closely correlate with the average growing season δ^2H_p signature of the wintering site (Hobson and Wassenaar 1996). Therefore, with the knowledge of moult timing and characteristics, the analysis δ^2H_f can provide information on migratory origin.

The absolute masses of each stable hydrogen isotope in a sample is difficult to measure precisely, however, minute difference in the ratio of heavy and light isotopes can be measured precisely (Hobson and Wassenaar 2008). Because of this, isotope measurements are generally presented as a value relative to an international standard using "δ" notation. For hydrogen, values are calculated as the measured ratio of deuterium/protium isotopes in a sample, divided by the measured ratio of the deuterium/protium of the standard -1, all multiplied by 1000 (Hobson and Wassenaar 2008).

1.5.4 Body composition analysis

Precise information on fat load is crucial to assessing factors that may govern migratory behaviour. Quantitative magnetic resonance (QMR) can be used to measure the fat and lean mass of captured birds (Guglielmo et al. 2011). QMR is a non-invasive method that uses magnetic resonance to quantify the mass (±0.01 g) of fat, lean wet tissue, free water, and total water in a specimen. During a QMR scan, a magnetic field is used to orient the spin of hydrogen nuclei in a subject. Antennae are then used to apply alternating magnetic fields at characteristic resonance frequencies to perturb the spin of the hydrogen nuclei into a higher energy state. When the magnetic field transmission is turned off, the spin of the hydrogen nuclei relax back into an equilibrium state, releasing energy at the same frequency as the initial stimulating frequency. The signal amplitude and the characteristics of the T1 and T2 relaxation curves provide information about the

physiochemical properties of the sample tissue, providing a method to distinguish and quantify fat mass, wet lean tissue mass, and free water (Taicher et al. 2003).

1.6 Study Species

The White-throated Sparrow (*Zonotrichia albicollis*) is an excellent species with which to examine differential migration timing and its underlying mechanisms with respect to sex, age, and behaviour. The White-throated Sparrow is a short distance migrant that breeds in the temperate and boreal forests of Canada and the northern United States (Figure 1) (Falls and Kopachena 2010). In addition to sex and age, a unique dimorphism exhibited by the White-throated Sparrow may also influence migration. In alternate breeding plumage, the colour of the median crown stripe and eyebrow stripe of both sexes can be used to distinguish birds as either a white-striped, or tan-striped morph (Lowther 1961). This dimorphism results from a difference in the second autosomal chromosome between morphs. Tan-striped birds have homologous acrocentric second chromosomes, whereas white-striped birds have one acrocentric and one metacentric second chromosome (Thorneycroft 1966, 1975). The dimorphisms in the second chromosome is thought to have resulted from multiple large-scale inversion mutations, consisting of around 1000 genes. These inversions suppress recombination during meiosis (Thomas et al. 2008), allowing for the divergence of distinct morphs and creating an additional class of individuals within this species.

Sex, morph, and age influence dominance and aggression in the White-throated Sparrow, with some evidence suggesting that these behavioural differences affect competitive ability. Males and white-striped birds exhibit greater aggression and social dominance than females and tan-striped birds of the same sex during the spring (Harrington 1973, Ficken et al. 1978, Watt et al. 1984, Kopachena and Falls 1993). In antagonistic interaction observed at feeding stations during spring migration, white-striped birds were more often the aggressor (Ficken et al. 1978). On the breeding grounds, white-striped males vocalise more often than tan-striped males (Collins and Houtman 1999, Falls and Kopachena 2010) and are more likely to engage in aggressive territorial behaviours (Kopachena and Falls 1993). Female white-striped birds engage in

territorial defence around the same level as tan-striped males, with tan-striped females not participating in antagonistic territorial interaction (Kopachena and Falls 1993).

White-throated Sparrows mate disassortatively with respect to morph, with almost every breeding pair consisting of either a white-striped male mated to a tan-striped female, or a tan-striped male mated to a white-striped female (Lowther 1961, Thorneycroft 1975, Tuttle 2003). This disassortative mating likely helps to maintain the polymorphisms exhibited in this species, as offspring of the homozygous tan-striped birds and heterozygous white-striped birds have an equal chance of being either a white-striped, tan-striped, male, or female. Reproductive behaviour also differs by morph. White-striped males are more likely to intrude into neighbouring territories and attempt extra-pair copulations, while tan-striped males invest a greater amount of time in mate guarding and parental care (Tuttle 2003).

During spring migration, White-throated Sparrows exhibit a high degree of migratory protandry (Knapton et al. 1984, Mills 2005, Caldwell and Mills 2006, Mazerolle and Hobson 2007). Using a 24-year banding data set, Mills (2005) found that males arrived at the Long Point Bird Observatory (Long Point, Ontario, Canada) around 10 days earlier than females. Mazerolle and Hobson (2007) observed a similar pattern at the Delta Marsh Bird Observatory (Portage la Prairie, Manitoba, Canada) using a nine-year data set, with males arriving around one week earlier than females. The pattern of protandry observed at migratory stopover sites is also reported at breeding sites in Algonquin Provincial Park (Ontario, Canada) (Knapton et al. 1984). Male White-throated Sparrows generally winter further north than females (Odum 1958, Jenkins and Cristol 2002, Mazerolle and Hobson 2005, 2007), although this difference is not discrete (Piper and Wiley 1989). Spring migration initiation timing may also differ between sexes. Odum (1949) reported that male White-throated Sparrows departed wintering areas around two weeks earlier than females. Sexing was conducted on some individuals using wing chord and plumage colouration, however, the plumage dimorphism exhibited by the White-throated Sparrow had yet to be recognized at this time and this may have influenced the findings of their study. For example, the misclassification of white-striped

females as males could have potentially accentuated the difference in average departure date between males and females.

Migration timing appears to differ between morphs within each sex, although to a lesser and more variable degree compared to sex. Using six years of banding data Caldwell and Mills (2006) found that white-striped birds arrived around two days earlier than tan-striped birds, however, this pattern was only significant in females when sexes were considered separately. A similar pattern was observed at breeding sites in Algonquin Provincial Park (Ontario, Canada) (Knapton et al. 1984). Mazerolle and Hobson (2007) report a greater difference in migration timing between the morphs at Delta Marsh, Manitoba, with white-striped birds arriving around five days earlier than tan-striped morphs. Differences in migration speed between white-striped and tan-striped morphs have not been examined during spring migration, however, Brown et al. (2014) found that refuelling rate was significantly higher in the white-striped birds during fall stopover. Migration distance does not appear to differ between white-striped and tan-striped birds based on stable isotope analysis (Mazerolle and Hobson 2007).

There is little evidence suggesting that differential migration timing by age occurs in the White-throated Sparrow. In the fall, Brown et al. (2014) found no significant difference in arrival timing at the Long Point Bird Observatory. Some evidence suggests that age classes differ in total migration distance. Odum (1958) reported that all birds killed by collisions with a television tower located near Tallahassee, Florida, USA, were immature birds. Tallahassee is located in the southern portion of the White-throated Sparrow wintering range. Assuming adults and juveniles are equally susceptible to tower strike mortality, the absences of adults among the tower kills could suggest that juveniles are overwintering at lower latitudes compared to adults.

White-throated Sparrows exhibit no sexual dichromatism, preventing the assignment of sex using plumage characteristics. Previous studies conducted on White-throated Sparrows have generally relied on morphometric based methodologies to determine sex. This could potentially introduce bias into the analyses as often these methods cannot mutually exclude males from females. Numerous studies have shown

that male White-throated Sparrows arrive earlier than females. However, discrepancy exists between studies in the number of days males precede females, which may result from methodological differences in assigning sex. Mills (2005) excluded individuals with wing chords within the male-female overlap range, whereas Mazerolle and Hobson (2007) used a less stringent criteria for wing length that allowed for the inclusion of more individuals.

Mis-sexing or excluding birds with intermediate wing chords may potentially bias analyses of sex-specific migration timing and wintering location. Wing chord is one of the many factors that can influence flight energetics (Alerstam and Hedenström 1998, Åkesson and Hedenström 2007) with potential ramifications for overall migration speed and timing. Excluding birds with intermediate wing chords may artificially inflate the difference in migration timing between sexes. Males and females with intermediate wing chords may have intermediate flight costs, migration speeds, and migration timing compared to smaller females and larger males. This could ultimately result in an outward shift between male and female mean migration date and a larger than true difference in migration timing. Mis-sexing birds based on wing chord may artificially reduce the within-sex variance in migration timing, resulting in an accentuated difference between the sexes. For example, females with longer wing chords could arrive earlier due to reduced flight costs. However, using a wing chord based sexing criteria, these females may be wrongfully sexed as males. If this pattern were to occur with males, the combined reduction in variance between groups could result in the incorrect conclusion of group-specific migration timing. This problem could also confound the analysis of wintering latitude. Wing chord is often correlated to body size. As body size is a key component in the susceptibility hypothesis, separating males and females by wing chord may confound the effect of sex and body size on wintering latitude. For example, if large bodied females overwintering at more northern latitudes are misclassified as males, an effect of sex on wintering latitude may be found when the underlying mechanisms is in fact body size.

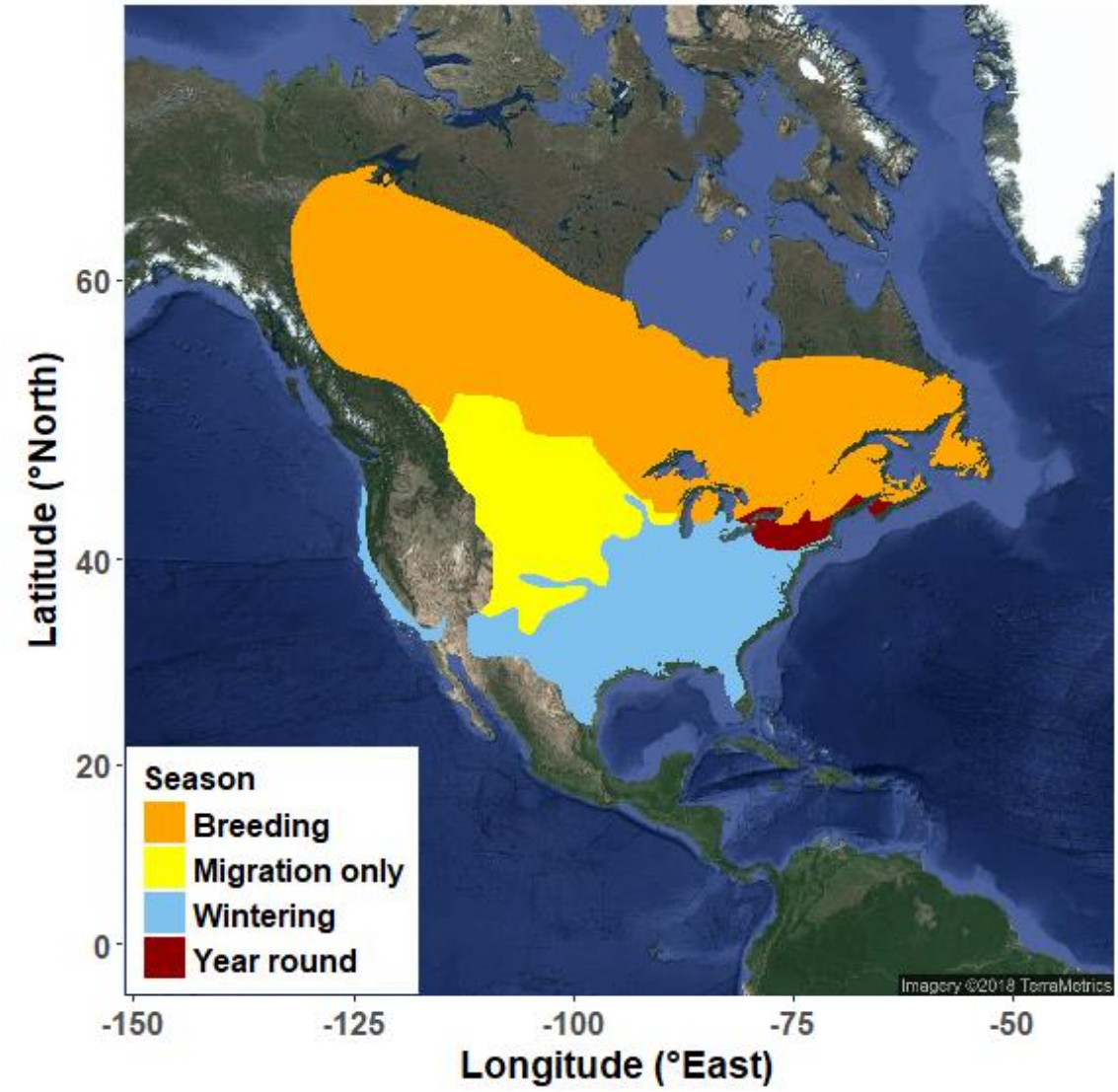

Figure 1. Range map of the White-throated Sparrow (*Zonotrichia albicollis*). Although breeding and wintering ranges overlap, all populations are migratory (Falls and Kopachena 2010). Provided by Birdlife International.

1.7 Study objective and overview

The objective of my thesis was to study differential spring migration timing in White-throated Sparrows. To approach this objective, I applied a suite of advanced techniques to examine differential migration timing (by sex, age, and morph) and its underlying behavioural mechanisms (refuelling rate, stopover duration, and wintering latitude). Migration timing at stopover was determined using capture data; plasma metabolite analysis and quantitative magnetic resonance was used to examine stopover refuelling rate and body condition; automated radio telemetry was used to determine stopover duration; wintering latitude was estimated using isotopic analysis of head feathers; and genetics was used to verify the sex and morph of individuals. By comparing migration timing, stopover refuelling rate, stopover duration, and winter latitude in the same season and at the same site, I hoped to explore how each behavioural mechanism contributed to the observed migration timing pattern.

Protandry is known to occur in the White-throated Sparrow, therefore I hypothesised that the behavioural mechanisms of migration timing would differ between the sexes. I expected that males would have a higher stopover refuelling rate and shorter stopover duration than females, which would result in males having a faster overall migration speed compared to females. Complementing this, I expected males to have a more northern wintering latitude, indicating a shorter overall migratory distance.

Morph-specific stopover ecology has not been examined during the spring, but in the fall, morph-specific refuelling rate has been demonstrated (Brown et al. 2014). Additionally, behavioural traits exhibited by white-striped plumage morphs may influence the competition for resources at stopover locations. Because of this, I expected that white-striped birds would have a higher refuelling rate than their same sex tan-striped counterparts. As higher refuelling rate may result in faster overall migration, I also expected white-striped birds to arrive earlier than tan-stiped birds of the same sex.

While latitudinal segregation by morph has not been demonstrated, other morph-specific migration behaviours do exist (Brown et al. 2014). The behavioural differences between the morphs, while not as prevalent during the non-breeding season, could potentially influence wintering latitude. Dominant white-striped individuals may

competitively exclude subordinate birds from more northern wintering areas, resulting in morph specific migration latitude within each sex. Additionally, molecular morphing and sexing techniques could help to reveal previously unrecognized patterns.

Differences in stopover refuelling rate between age classes are generally not observed in spring migrating songbirds, (Morris and Glasgow 2001, Morris et al. 2003, Morbey et al. 2018). As such, I expected no difference in refuelling rate to be observed between age classes. Several studies have demonstrated a difference in stopover duration between adult and juvenile songbirds. However, given a limited supply of radio transmitters, I elected to focus on adult birds only to increase the power to detect an effect of sex and morph. Finally, I expected juvenile White-throated Sparrows to overwinter at more southern latitudes. Dominant adults may competitively exclude subordinate juveniles from more northern wintering areas within each sex-morph class. Additionally, high proportion of juveniles in tower kills in the southern portion of the wintering range (Odum 1958) suggests that differential migration distance by age may occur in the White-throated Sparrow.

Methods

2.1 Study site

I studied White-throated Sparrows during migratory stopover on the Long Point peninsula located in Ontario, Canada (42°34'58.5"N 80°23'54.5"W). Long Point is situated between the Mississippi and Atlantic flyways, and possesses many characteristics that make it an ideal stopover site for migratory birds. Originating on the north shore of Lake Erie and extending eastward for over 25 km into the lake, Long Point is a likely location for birds traversing the lake to make landfall in the spring. Radar observations have shown that birds crossing the Great Lakes reorient towards the nearest land mass at dawn (Diehl et al. 2003), and this behaviour likely contributes to the high number of migratory birds concentrating in the Long Point area. A variety of habitat types that may attract migratory birds are present on the Long Point peninsula, including woodlands, sand dunes, marshes, ponds, meadows, beaches, and lakeshore (UNESCO). Indicators of habitat quality such as forest structure may be used by migrants to fine tune stopover habitat selection, with forest and riparian habitat (Bonter et al. 2009, Buler and Moore 2011, McCabe and Olsen 2015). Furthermore, the predominantly agricultural landscape of the north shore of Lake Erie may concentrate birds in the Long Point area, as it is thought that many songbirds actively avoid agricultural areas during migration (Bonter et al. 2009). Positive mass changes have been documented in birds stopping over in the Long Point area (Dunn 2000), indicating that Long Point provides suitable stopover habitat for many migratory bird species.

I captured White-throated Sparrows at the Long Point Bird Observatory's "Old Cut" banding station 42°34'58.5"N 80°23'54.5"W, located near Port Rowan, Ontario, between 9 April 2017 and 15 May 2017. The Old Cut banding station is situated in a small woodlot located near the base of the Long Point peninsula. Vegetation cover is a mix of medium density cottonwoods (*Populus deltoides*), and dense Red Pine (*Pinus resinosa*). Habitat surrounding the banding station includes highly vegetated medium density housing, and wet areas dominated by shrubs (e.g. red osier dogwood [*Cornus stolonifera*]) (Dunn 2000). Birds were captured following the Long Point Bird

Observatory Migration Monitoring Protocol (LPBO 2005). An array of 15 mist nets was opened 30 minutes before sunrise, and remained open for six hours each day (weather permitting). All birds captured at Old Cut, either by myself of the bird observatory staff, had a standard Canadian Wildlife Service aluminium leg band affixed around the tarsus. Weight and un-flattened wing chord were measured, and age (SY= second year [juvenile]; ASY = after second year [adult]), sex, and morph were provisionally assigned using plumage characteristics (Piper and Wiley 1991, Pyle 1997, Caldwell and Mills 2006) and later validated the field assignments using genetic analysis (described below). Sex was provisionally assigned following Piper and Wiley (1991), with birds possessing an un-flattened wing chord greater than 70 mm assigned as males and all other birds assigned as females. This sexing criteria allows for the assignment of sex to all birds and is approximately 90% accurate. Some birds were processed by the Old Cut banding station, and I attempted to collect data on as many of these birds as possible by retrieving them after they had been processed by the banding station. To avoid repeated sampling, I did not sample any birds that were captured with a leg band. Crown stripe feathers (0.7 g) and one of the innermost rectrices were taken, placed in labelled envelopes, and frozen for isotopic and genetic analysis (described below). Prior to release, I used quantitative magnetic resonance to measure body composition (Guglielmo et al. 2011). Birds were scanned in an Echo-MRI-B (Echo-Medical Systems, Houston, TX, USA). The QMR scanner was calibrated once daily using a 94 g canola oil standard. Exposure to strong magnetic fields during QMR does not negatively affect stopover duration or post departure movement (Kennedy et al. 2016). All birds were scanned once on the “small” bird and two accumulation software settings, and fat and lean mass were corrected using equations in Guglielmo et al. (2011) prior to analysis. Field work was conducted under Canadian Wildlife Service permit number CA-0255 with the approval of the University of Western Ontario’s animal care committee (protocol # 2010-020) (Appendix 1).

2.2 Assessment of stopover refuelling performance

Plasma metabolite analysis was used to assess stopover refuelling performance in a subset of White-throated Sparrows. Starting one hour after local sunrise, mist nets were monitored, and sparrows observed entering a mist net were selected for blood sampling.

A timer was used to measure the elapsed time between capture and the beginning of blood extraction (bleed time), with all bleed times being less than 11 minutes. Blood samples were taken immediately following capture to best reflect the profile of a feeding bird, as plasma metabolite concentrations can be rapidly affected by behavioural changes (Guglielmo et al. 2002, Zajac et al. 2006). Up to 300 µl of blood (approximately 10% total blood volume) was sampled from the brachial vein into a heparinized microvettes (Sarstedt Microvette CB 300, 16.443.100). Immediately following, blood samples were centrifuged at 2000 g for 10 minutes to separate plasma. Plasma was then transferred into screw-top cryogenic tubes and stored in a liquid nitrogen dry shipper (Taylor-Wharton CX 100). Samples were transported bi-weekly to the University of Western Ontario and were stored at -80°C for three months until analysis.

Metabolites were measured using colorimetric assays following Guglielmo et al. (2002, 2005). Assays were conducted on a microplate spectrophotometer (Biotec Powerwave X 340) in 400 µl flat-bottom microplates (Nunc, Roskilde, Denmark). Plasma β-OH Butyrate concentration was determined using kinetic endpoint assay (R-Biopharm, kit number 10907979035). This assay uses nicotinamideadenine dinucleotide (NAD) to oxidise β-OH Butyrate to acetoacetate in the presence of the enzyme 3-hydroxybutyrate dehydrogenase. Reduced NAD from this reaction then converts iodonitrotetrazolium chloride (INT) to a formazan dye which is measured at 492 nm. To conduct the assay, five µl of plasma and 200 µl of a working solution containing NAD, diaphorase, and INT in a potassium phosphate/triethanolamine buffer were added to each well, and ΔA/min was measured for 2 minutes at 492 nm to check for a high background reaction rate. Four µl of B-OH-butyrate dehydrogenase suspension was then rapidly added to each well using a positive displacement repeat pipette (Eppendorf). ΔA/min was then measured for the next 40 minutes at 492nm. Background was adjusted for by subtracting three times ΔA 30-40 min from ΔA 0-30 min. Final concentrations were calculated against the linear standard curves constructed using standards ranging from 0.15-3.17 mmol*L^{-1} concentrations of β-OH Butyrate (Stanbio 2450-604).

Plasma gylcerol and triglyceride concentration were determined using sequential endpoint assay (SIGMA, Trinder reagent A and B). This assay measures the concentration of triglyceride through the enzymatic production of glycerol from triglyceride, followed by a series of reactions that produce a quinoneimine dye absorbed at 540 nm (Trinder 1969, Barham and Trinder 1972, Bucolo and David 1973). The reaction involves the glycerol kinase (GK) mediated phosphorylation of glycerol by adenosine-5'-triphosphate (ATP) to produce glycerol-1-phosphate (G-1-P) and adenosine-5'-diphosphate (ADP). G-1-P is then oxidised by glycerol phosphate oxidase (GPO) to produce dihydroxyacetone phosphate and hydrogen peroxide (H_2O_2). Peroxidase (POD) then catalyses a reaction between H_2O_2, 4-aminoantipyrine (4-AAP), and sodium N-ethyl-N-(3-sulfopropyl) m-anisidine (ESPA) to produce quinoneimine dye. The absorbance at 540 nm is proportional to the glycerol concentration of the sample. To measure triglyceride concentrations, free glycerol concentrations are measured, followed by the addition of lipoprotein lipase to hydrolyse triglyceride to glycerol and free fatty acids. The difference between the initial free glycerol and final total triglyceride corresponds to the true triglyceride concentration. Five µl of plasma, and 240 µl of reagent A (containing the GK, ATP, GPO, POD, 4-AAP, and ESPA) was added to each well and incubated at 35° C for 10 minutes. Afterwards, absorbance was measured at a primary wavelength of 540 nm to determine the plasma free glycerol concentration. Next, 60 µl of solution B (containing the lipoprotein lipase) was added to each well and incubated for 10 minutes, following which absorbance was measured at the same wavelengths to determine the plasma triglyceride concentration. Final concentrations were calculated against the linear standard curves constructed using standards ranging from 0.176 – 5.64 $mmol*L^{-1}$ concentrations of glycerol (Sigma G7793). Most samples were assayed in duplicate with undiluted plasma, and the average concentration was used for analysis. Duplicates with a coefficient of variation (CV) greater than 15% were assayed a third time to improve estimate accuracy. Samples with low plasma volumes were diluted with 0.09% saline and in four cases were run without duplicate. True triglyceride was calculated by subtracting the measured glycerol from total triglyceride.

2.3 Assessment of stopover duration

To determine stopover duration, I deployed radio tags on birds while attempting to balance the number of tags by sex, morph, and date. To increase the power to detect an effect of sex and morph given a limited supply (N= 59) of radio transmitters, I elected to focus on adult birds only. Birds were captured and processed following the above methods, and tagged with digitally encoded radio transmitter tags (model NTQB-1, Lotek Wireless, www.lotekwirelss.ca) set to emit a uniquely encoded radio pulse every 12.7 s. Tags weighed approximately 0.29 g (< 2% body weight) and were affixed using a leg loop harness (Rappole and Tipton 1991) (Figure 2). Harnesses were constructed out of elastic thread (Dritz, 11345W), which was glued to the radio tag using cyanoacrylate glue (Bob Smith Industries Inc. Instacure +, www.bsi-inc.com). Total harness length was determined based on mass at capture, and ranged between 41 mm and 47 mm. Birds selected for radio tagging did not have blood samples taken.

Stopover duration was measured using the Motus Wildlife Telemetry System (Taylor et al. 2017). The detection of a tagged birds radio signal on Motus towers within the stopover landscape was used to indicate that bird was still on stopover. To accommodate for short distance relocations known to occur during stopover (Taylor et al. 2011, Dossman et al. 2016), any site within 20 km of Old Cut was considered within the stopover landscape. Departure night from stopover was considered as the last night a bird was detected on a tower within the stopover landscape. Stopover duration was calculated as (departure night – capture day + 1), providing the minimum duration of the stopover bout (Dossman et al. 2016).

Figure 2. Lotek NTQB-1 radio transmitter tag affixed to the back of a White-throated Sparrow using a leg-loop harness.

2.4 Stable isotope analysis

2.4.1 Assessment of wintering latitude

To examine the influence of sex, age, and morph on wintering latitude, stable hydrogen isotopes analysis was conducted on collected head feather samples (Wassenaar and Hobson 2003, Mazerolle and Hobson 2007). White-throated Sparrow undergo a partial moult (pre-alternate moult) on the wintering grounds prior to spring migration, which includes body and head feathers (Pyle 1997). Head feathers sampled during spring migration therefore act as a tracer of wintering latitude. Analysis of feather stable hydrogen isotopes (δ^2H_f) was conducted using continuous flow-isotope ratio mass spectrometry (Mazerolle and Hobson 2007, Hobson 2011). Feathers were washed with a 2:1 chloroform: methanol solution to remove surface oil contamination, and allowed to air dry overnight. Prior to weighing, the calamus was removed from all head feathers to ensure that there was no hydrogen input from remnant feather follicles. Head feathers were weighed (0.35 ± 0.03 mg) into silver capsules (Elemental Microanalysis D2000). Prior to analysis, feather samples and standards were passively co-equilibrated with ambient laboratory air for around two weeks to control for hydrogen exchange between feathers and ambient water vapour (Wassenaar and Hobson 2003).

Analysis was conducted at the LSIS-AFAR stable isotope laboratory at Western University, Ontario, Canada. Pyrolysis of feather samples was conducted using a Thermo Finnigan High-temperature Conversion-Elemental Analyser (TC-EA) with a chromium packed reactor. Chromium reactors reduce the error in the measured δ^2H_f values by preventing the formation of hydrogen cyanide during pyrolysis of nitrogen rich feathers (Reynard and Tuross 2016). Measurement of δ^2H_f values was carried out using a Thermo Delta V Plus mass spectrometer. Measured δ^2H_f values were normalised to VSMOW (Vienna Standard Mean Ocean Water) international standard scale, and are expressed in parts per thousand (‰) (Hobson and Wassenaar 2008). Environment Canada keratin reference standards CBS (Caribou hoof: -197‰) and KHS (Kudu horn : -54.1‰) were used to calibrate measured δ^2H_f values.

2.4.2 Assigning birds to geographic origin

The geographic origin of sampled birds was assigned using the likelihood method (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011), using an R script provided by Environment and Climate Change Canada in R version 3.4.3 (R Core Team 2017). A GIS-based map of mean growing season precipitation stable hydrogen isotopes (δ^2H_p) (Bowen et al. 2005) was first calibrated to produce a map (isoscape) of expected feather stable hydrogen isotope (δ^2H_f) values for ground foraging short distance migrants, using the equation $\delta^2H_f = -22.9808 + 0.9527\ \delta^2H_p$ (Hobson et al. 2012). The feather isoscape was then cropped to include only known wintering location of White-throated Sparrows (BirdLife International) using the mask function in the 'raster' R package (Hijmans 2017).

To depict the likely migratory origin of each sex, morph, and age group, each bird was assigned to the base map one at a time. First, the probability of each bird originating from each cell in the raster feather isoscape was determined using a normal probability density function. Individual δ^2H_f values were compared to each cell in the raster feather isoscape, considering the estimated standard deviation of 18.4‰ for short distance ground foraging birds growing head feathers in the same location (Hobson et al. 2012). Next, a 2:1 odds ratio was used as a threshold to assess if a bird had originated from each cell in the raster feather isoscape. The resulting range represented areas where the likelihood of origin was greater than 67% for that individual. Cells within this range were coded as one, while cells that did not meet the likelihood threshold were coded as a zero. Once this process was completed for all birds, cell values were summed for all individuals, providing the number of individual with a 67% likelihood of originating from each cell in the feather isoscape. This value was standardised to the total number of individuals in the data set, to provide a raster map of the percent of measured individuals with a 67% likelihood of originating from each cell.

2.5 Genetic analysis

2.5.1 DNA extraction from red blood cell

Packed erythrocytes (5 µl) were placed in 300µl of TNES buffer (50 mM Tris-HCl pH 8.0, 25 mM EDTA, 100 mM NaCl, 2% SDS) with 100 µg of proteinase-K (P2308 Sigma), and incubated at 55°C for 3 hours. Lysis mixture was then mixed vigorously with 300 µL of 25:24:1 phenol/chloroform/isoamyl alcohol saturated with EDTA (P2069 Sigma), and centrifuged at 5000 g for 5 minutes. DNA containing supernatant was collected into 1.5 ml centrifuge tubes. DNA was then precipitated by adding 25 µl of sodium acetate (3 M, pH 5.2) and 300 µl of chilled ethanol, and incubating at -20 for 18-24 hours. The DNA mix was then centrifuged at 15000 g for 30 minutes at 4°C to form a solid pellet of DNA. Ethanol was discarded from each tube, and DNA pellets were washed by adding 1 mL of 70% ethanol, inverting the tubes ten times, and then centrifuging at 15000 g for 5 minutes. Pellets were then washed again following the same process, following which residual ethanol was aspirated. DNA was solubilized with 50 µl of DNAase free water and DNA concentration was determined. DNA was then diluted to a final concentration of 20 ng/µl.

2.5.2 DNA extraction from feathers

To extract genomic DNA from tail feathers, sterile razor blades were used to separate the calamus 15 mm from the base of the feather, and bisected longitudinally to expose interior pulp cells. Feather sections were placed in 300 µl of TNES buffer (50 mM Tris-HCl pH 8.0, 25 mM EDTA, 100 mM NaCl, 2% SDS) with 100 µg of proteinase-K (P2308 Sigma), and incubated at 55°C for 18 hours. Lysis mixture was then mixed vigorously with 300 µl of 25:24:1 phenol:chloroform:isoamyl alcohol [saturated with EDTA] (P2069 Sigma), and centrifuged at 5000 g for 5 minutes. DNA containing supernatant was collected into 1.5 ml centrifuge tubes. DNA was then precipitated by adding 25 µl of sodium acetate (3M, pH 5.2), 250 µl of chilled isopropanol, 2 µl of Glycoblue (AM9515, ThermoFisher), and incubating at -20 for 18-24 hours. DNA was solubilized with 25 µl of DNase free water and DNA concentration was determined using

a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific). DNA was then diluted to a final concentration of 20 ng/µl.

2.5.3 DNA amplification

All PCR reactions were performed in 20 µl volumes in a 200 µl PCR tube using a Rotor-Gene Gene-Disc^{TM} 6000 (Corbett Research). PCR reaction mixture consisted of 3 µl of genomic DNA, 1x PCR buffer, 2 mM $MgCl_2$, 0.2 mM dNTP (Each), 0.2 µM forward and reverse primers, and 1 unit of Taq DNA polymerase. PCR thermal cycle conditions were 94**°**C for 1 minute (initial denaturing), 40 cycles of; 94°C for 30s, 48**°**C for 45s, and 72°C for 45s, and 72°C for 5 minutes (final extension). PCR products were separated on a 3% agarose gel pre-stained with Sybersafe (S33102 Thermofisher Scientific) in 1x TAE buffer. Molecular sexing was conducted using the P2/P8 (Griffiths et al. 1998) and CHID-W/CHID-Z (Morbey et al. 2018) primer sets. Both the P2/P8 and CHID-W/CHID-Z primers target sequences associated with chromobox-helicase-DNA-binding gene, and simultaneously amplify sequences located on the avian W and Z sex chromosomes. The amplified sequences produced from the W and Z chromosomes differ in length. P2/P8 produce a single (~350 bp band) for homozygous ZZ males and pair of bands (~350 bp and ~400 bp) for heterozygous WZ females. CHID-W/CHID-Z (forward, 5'-GTATCGTCAATTTCCATTTCAGGT-3'; reverse, 5'-CCATCAAGTCTCTAAAGA-GATTGA-3') produce a single band (520 bp) for males and pair of bands (520 bp and 319 bp) for females. Molecular morph determination was conducted using the Dra*I* RFLP genotype assay (Michopoulos et al. 2007). A 285 bp sequence was first amplified using the primer set described by Michopoulos et al. (2007) (forward, 5'-CAGAGCTATGGAACATGAAC-AAC-3'; reverse, 5'-AACTGTAGCTCCTGCACATTCTC-3'). Ten µl of PCR product was then digested for 2 hours at 37°C using 20 units of Dra*I* in 1x of Cutsmart^{TM} buffer (New England Biolabs). Digested and undigested PRC products were run in parallel on 3% agarose gel. The sequence amplified by the primers contains the recognition sequence required for cleavage by Dra*I* in white-striped birds only, resulting in bands at 200 bp and 85 bp. Tan-striped birds yield a single band at 285 bp.

2.6 Statistical analysis

2.6.1 Capture timing and body composition analysis

To examine differential migration timing, I analysed a general linear model of capture date with sex, morph, age. To test for differences in body condition between groups of birds, separate general linear models were conducted for total body mass, fat mass, and lean mass using sex, morph, and age as factors with day of year and time since sunrise included as covariates. Time since sunrise was calculated as the difference between capture time and civil sunrise. The inclusion of two-way interactions between the factors sex, morph, and age were considered using likelihood ratio tests (Myers 1990) between the model containing all single variable terms, and the model including all single variable terms and a two-way interaction with a critical value of 0.05. If model fit was not significantly improved by the inclusion of a two-way interaction term, the interaction was not included when assessing the effects of the single term variables. Model assumptions were examined visually by plotting model residual by predicted values and with a residual quantile-quantile plot. Variance homogeneity and residual normality were tested using Levene's tests and a Shapiro-Wilk test respectively.

2.6.2 Refuelling rate analysis

Metabolite concentrations were $\log_{10}$([metabolite]) +1 transformed to satisfy normality assumptions, and to conform to previous studies. Principal component analysis was used to create a refuelling index (RI) useful for comparative analysis (Guglielmo et al. 2005). Triglyceride and β-OH butyrate values were examined for correlation between each other, and with bleed time. A general linear model was used to test for the effect of sex, morph, and age on RI. Fat mass, lean mass, day of year, time since sunrise, and daily White-throated Sparrow abundance (henceforth competitor abundance) was included in the model as a covariate and was estimated from total daily sightings and captures by LPBO personnel. Competitor abundance was included in the model to test if the abundance of White-throated Sparrows at Old Cut may have influenced refuelling rate. The inclusion of two-way interactions between the factors sex, morph, and age were considered following the method described above. Model assumptions were examined

visually by plotting model residual by predicted values and with a residual quantile-quantile plot. Variance homogeneity and residual normality were tested using Levene's tests and a Shapiro-Wilk test respectively.

2.6.3 Stopover duration analysis

To test for differences in stopover duration, Cox semiparametric hazard regression was applied in a proportional hazard modelling framework using SAS software's PHREG procedure (Dossman et al. 2016, Morbey et al. 2018). Proportional hazard analysis provides a method to examine how factors and covariates affect the length of time that passes before the occurrence of an event. Covariates that shorten the time elapsed before the occurrence of an event are said to increase the "risk". In the context of avian migration and migratory stopover, departure from stopover is the event of concern. High departure "risk" indicates a higher probability of leaving a stopover site and a shorter stopover duration. Conversely, lower "risk" of departure translates to a low probability of leaving, and a longer stopover duration. Hereafter, "risk" will refer to the probability of departure. Procedure PHREG allows for the inclusion of time-dependent covariates, providing a method to explicitly examine how temporally variable environmental conditions affect the risk of departure. Tailwind, temperature, and competitor (i.e. White-throated Sparrow) abundance were included as time dependent covariates in the model of departure risk. Several studies have found a positive association between tailwind and departure from stopover (Kemp et al. 2010, Sjöberg et al. 2015, Dossman et al. 2016, Morbey et al. 2018), and temperature is known to influence migratory restlessness in captive White-throated Sparrows (Metcalfe et al. 2013). Competitor abundance was included to test if the density of White-throated Sparrows at Old Cut may have influenced departure risk.

Tailwind values were assigned for each day a bird was at risk of departure following Morbey et al. (2018). Wind data was obtained from the NCEP/DOE Reanalysis 2 data set (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html) which provides meteorological data four times each day at 2.5° x 2.5° spatial resolution. Wind speed in $m \cdot s^{-1}$ in the easterly and northerly direction was extracted using the RNCEP package in R (Kemp et al. 2012), and interpolated for Old Cut (lat = 42.583°, lon = -

80.397°) using the function NCEP.interpol with the option for linear interpolation. Wind was interpolated for 1000 mb pressure level at sunset (https://www.nrc-cnrc.gc.ca/eng/services/sunrise/ index.html). Tailwind component was estimated as V_w*cos(β), where V_w is wind speed ($m \cdot s^{-1}$) and β is the difference between flight bearing and wind direction. Flight bearing was assumed to be North (0°). Temperature for each day a bird was at risk of departure was represented as the average daily temperature over a 24-hour period from midnight. Temperature data was recorded during the field season every five minutes using a temperature sensor (Onset S-THB-M002) connected to an Onset Hobo Micro Station (H21 -002) located in the Old Cut woodlot. During the spring, tailwind and temperature likely show strong correlation, with warmer southern tailwinds and cooler northern headwinds. To control for multicollinearity between tailwind and temperature, I first tested for correlation between tailwind and temperature, following which I conducted a principal component analysis on tailwind and temperature using the PRINCOMP procedure in SAS.

Proportional hazard analysis was conducted using a model containing sex and morph as factors, with fat mass, lean mass, and day of year included as covariates. The first component of a PCA of tailwind and temperature was included as time-dependent covariates to account for environmental variability. Competitor abundance was also included in the model as a time-dependent covariate. The exact method was specified to handled tied stopover durations between individuals. This method calculates the probability of departure as the sum of the probabilities of all potential order combinations between tied individuals, and provides a more precise estimate of departure risk. Difference in stopover duration between sex and morph classes was visualised using separate Kaplan-Meier survival estimator plots.

2.6.4 Wintering latitude analysis

Wintering latitude was examined using head δ^2H_f values, with lower values indicating a more northern wintering latitude. Because a small percentage of head feathers can be retained during the pre-alternate moult, samples with δ^2H_f values less than those expected within the known winter range of the White-throated Sparrow (–85‰) were excluded from the analysis (Mazerolle et al. 2005). A general linear model of δ^2H_f values was

analysed to test if wintering latitude was influenced by the factors sex, morph and age. The inclusion of two-way interactions between the factors sex, morph, and age were considered using a likelihood ratio test as described previously. Model assumptions were examined visually by plotting model residual by predicted values and with a residual quantile-quantile plot. Variance homogeneity and residual normality were tested using Levene's tests and a Shapiro-Wilk test respectively. All statistical analyses were performed in SAS v. 9.4. (SAS Institute 2015) or R v. 3.4.3 (R Core Team 2017).

Results

A total of 421 birds were sampled between 9 April 2017 and 15 May 2017, consisting of 83 birds sampled for plasma metabolite analysis, 53 birds radio tagged, with the remaining 285 birds feather sampled only. Difficulties conducting genetic analysis using DNA extracted from feathers precluded the assignment of sex and morph of some birds. Sex was determined for 141 birds and morph was determined for 239 birds, with sex *and* morph confirmed for 119 birds using genetic analysis. Age was confidently determined in the field for 112 of these 119 birds. Validation of the provisional field assignment of sex and morph yielded an accuracy of 91% for sex, and 89% for morph.

3.1 Migration timing

First capture date was modelled for 112 birds with positively confirmed sex, morph, and age. Likelihood ratio tests indicated that none of the two-way interactions between sex, morph, and age increased model fit (all $p > 0.05$). A general linear model containing sex, morph, and age was highly significant ($F_{3,108} = 24.29$, $p < 0.0001$). Sex signficantly influenced first capture date ($F_{1,108} = 70.72$, $p < 0.001$), with males preceeding females by 11 ± 1.3 days (Figure 3). First capture date was unaffected by morph ($F_{1,108} = 0.01$, $p > 0.5$), with equal mean first capture dates between white-striped and tan-striped birds (Figure 4). Age did not have a signficant influence on migration timing ($F_{1,108} = 0.01$, $p > 0.5$) (Figure 5**).**While Levene's tests indicated that the assumption of variance homogenity was met (all $p > 0.05$), a Shapiro-Wilk test suggested that the distribution of the model residuals departed from normaility ($W = 0.96$, $p = 0.006$). Inspection of the model diagniostic plots (Figure 6) suggested that this may have resulted from a few late arriving individuals, and likely does not constitue a major violation of a model assumption given the sample size of 112.

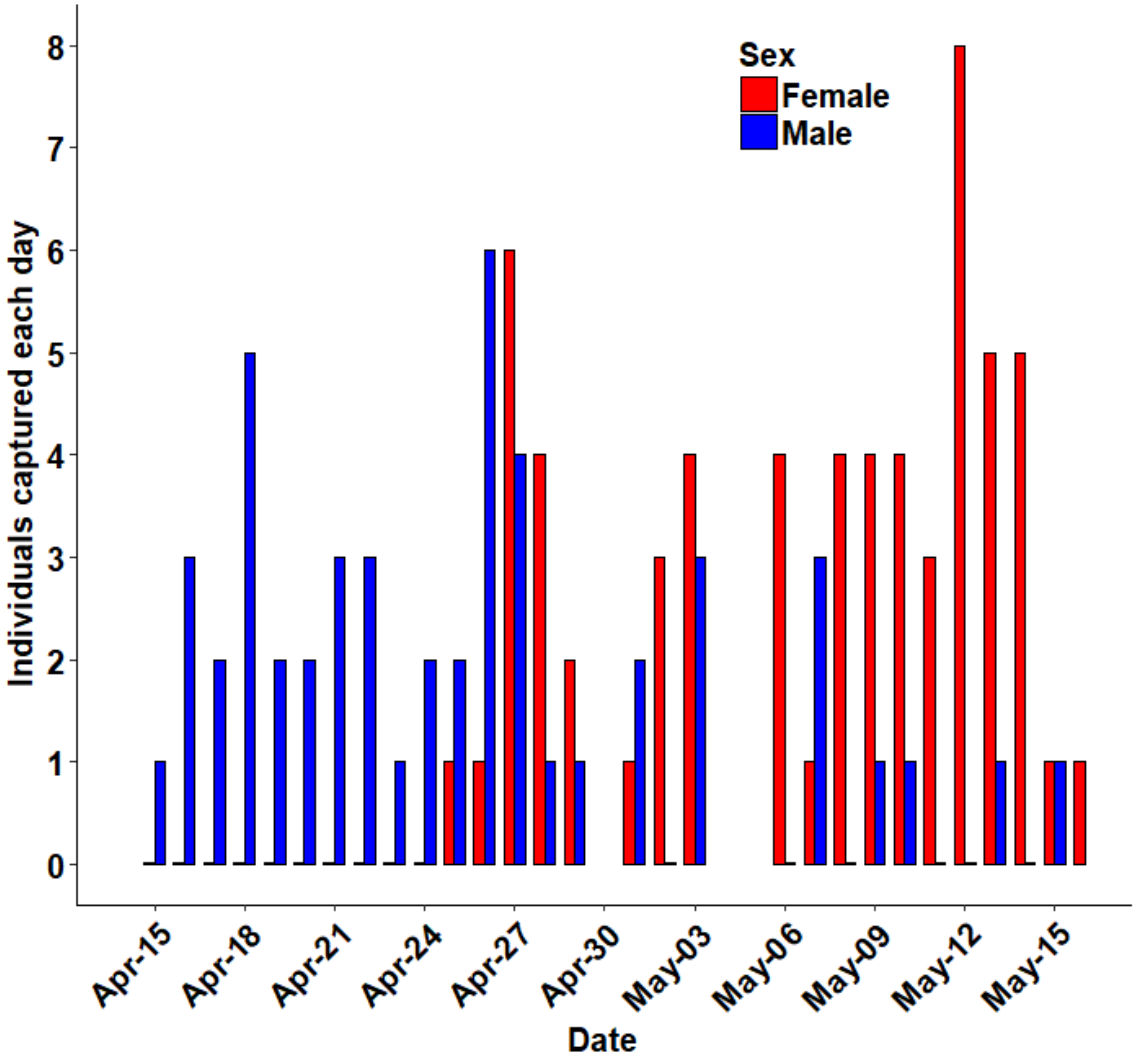

Figure 3. Distribution of first capture date at the Long Point Bird Observatory, Long Point, Ontario, Canada, for male (N = 50) and female (N = 62) White-throated Sparrows (*Zonotrichia albicollis*) during spring migration 2017.

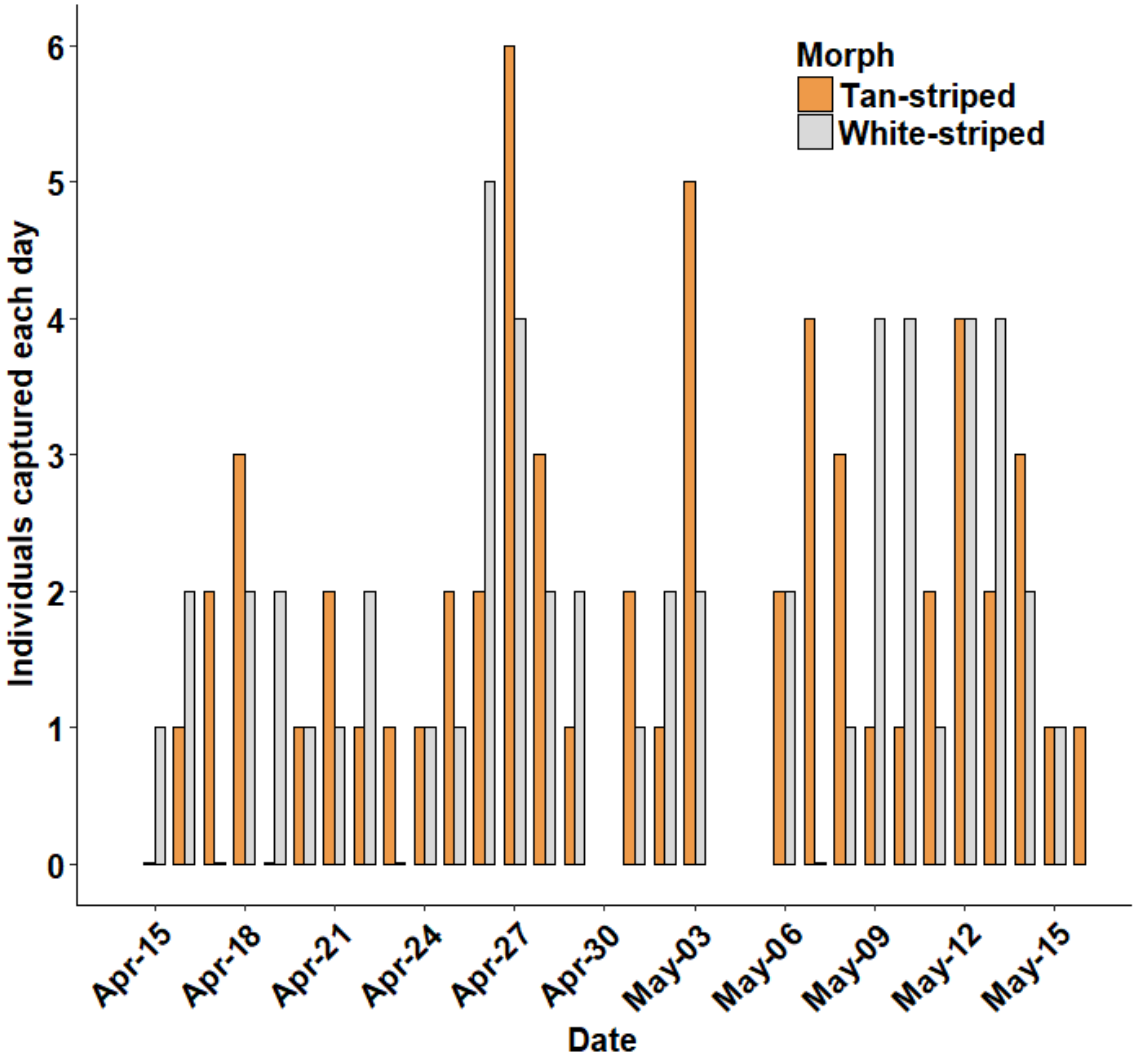

Figure 4. Distribution of first capture date at the Long Point Bird Observatory, Long Point, Ontario, Canada, for white-stiped (N = 54) and tan-striped (N = 58) White-throated Sparrows (*Zonotrichia albicollis*) during spring migration 2017.

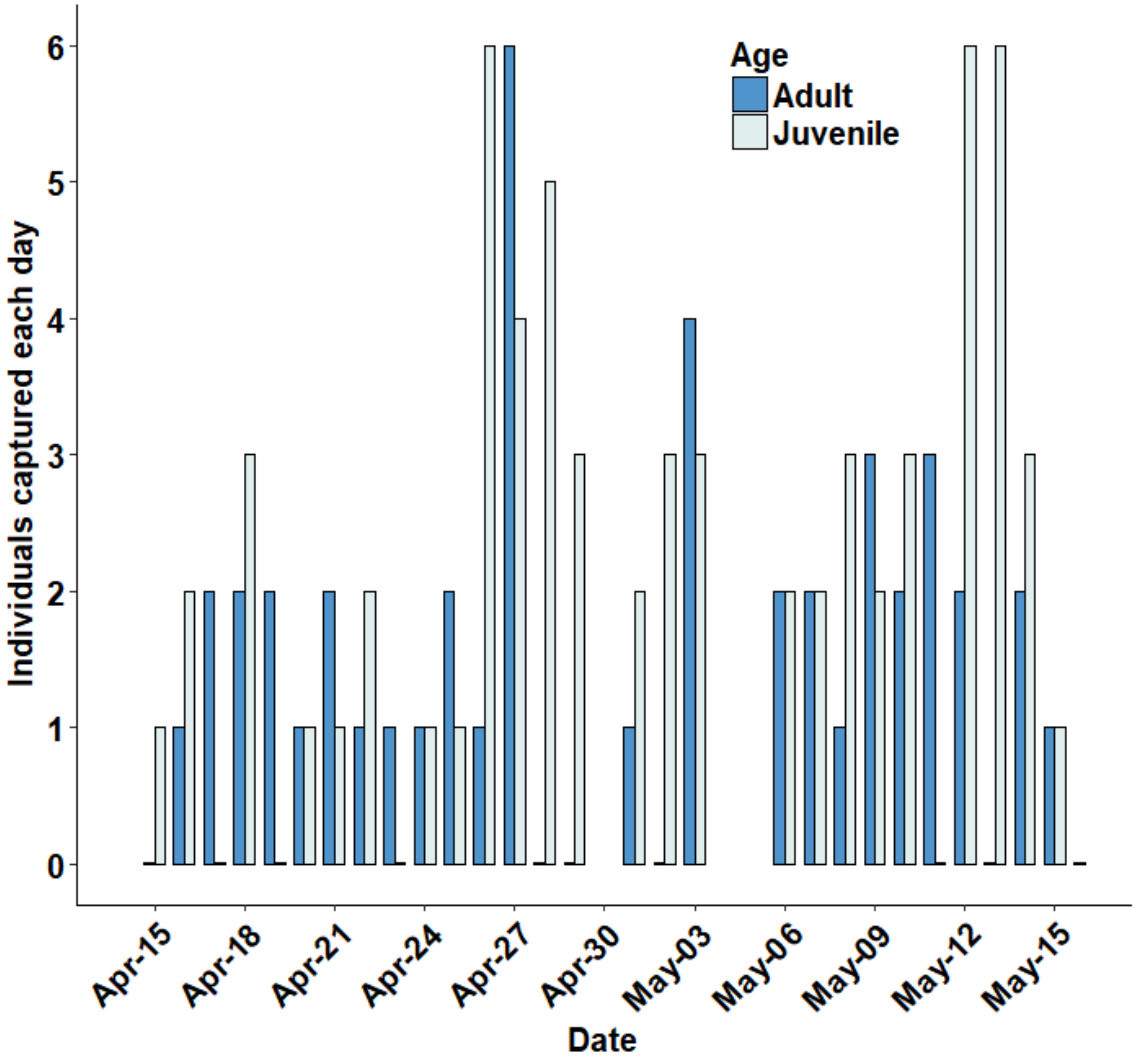

Figure 5. Distribution of first capture date at the Long Point Bird Observatory, Long Point, Ontario, Canada, for adult (after-second-year) (N = 54) and juvenile (second-year) (N = 62) White-throated Sparrows (*Zonotrichia albicollis)* during spring migration 2017

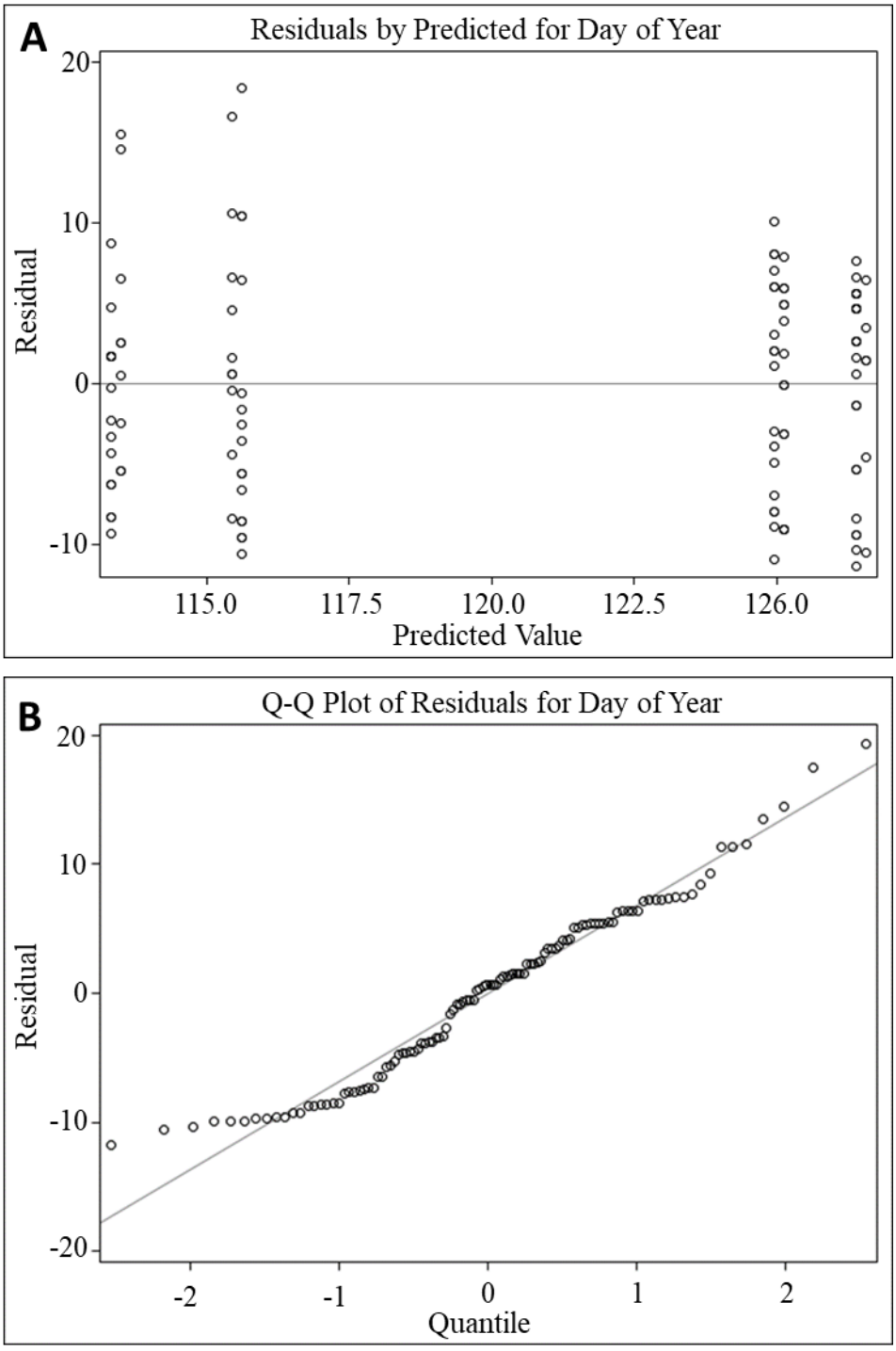

Figure 6. Model residuals by predicted values (A), and residual quantile-quantile plot (B) for the general linear model of capture date for White-throated Sparrows (*Zonotrichia albicollis*) migrating through Long Point, Ontario, Canada, during the spring of 2017.

3.2 Body Composition

Individuals of different age and sex classes differed in body mass, fat mass, and lean mass. Total body mass was modelled for 106 individuals. Likelihood ratio tests indicated that none of the two-way interactions between sex, morph, and age increased model fit (all $p > 0.05$). The model of total mass containing sex, morph, age, day of year, and time since sunrise was highly significant ($F_{5,100} = 10.41$, $p < 0.0001$, $R^2 = 0.34$). Total body mass was significantly different between sexes ($F_{1,100} = 36.65$, $p < 0.0001$), ages ($F_{1,100} = 4.57$, $p = 0.035$), and depended on the day of year ($F_{1,100} = 13.38$, $p < 0.001$) and time since sunrise ($F_{1,100} = 2.19$, $p = 0.025$). Total body mass did not differ between morphs ($p > 0.1$). Total body mass of males was 3.45 ± 0.6 g greater than females, 0.93 ± 0.4 g higher in adults compared to juveniles and increased 0.1 ± 0.03 g with each day of the year and 0.004 ± 0.002 g with every minute since sunrise (Table 1).

Fat mass was modeled for 103 individuals. The model of fat mass containing sex, morph, age, day of year, and time of day was highly significant ($F_{5,97} = 9.87$, $p = 0.0001$, $R^2 = 0.34$), and was not improved by the inclusion of interaction terms (all $p > 0.05$). Fat mass differed between the sexes ($F_{1,97} = 19.04$, $p < 0.001$), and depended on the day of year ($F_{1,97} = 47.88$, $p < 0.001$.) Fat mass did not differ between morph ($p = 0.9$) or age classes ($p = 0.3$) and did not depend on the time of day ($p = 0.5$). Fat mass was 1.60 ± 0.4 g higher in males, and increased by 0.14 ± 0.02 g for each day of the year (Table 1).

Finally, lean mass was modeled for 103 individuals. The model of lean mass containing sex, morph, age, day of year, and time of day was highly significant ($F_{5,97} = 19.34$, $p = 0.0001$, $R^2 = 0.50$), and was not improved by the inclusion of interaction terms (all $p > 0.05$). Lean mass differed between the sexes ($F_{1,97} = 39.09$, $p < 0.001$) and depended slightly on time since sunrise ($F_{1,97} = 8.58$, $p = 0.004$). Lean mass did not differ between morph ($p = 0.9$) or age classes ($p = 0.07$), and did not depend on the day of year ($p = 0.9$). Lean mass was 1.83 ± 0.3 g higher in males compared to females, and increased 0.003 g with every minute since sunrise (Table 1). Model assumptions were satisfied in all body composition analyses.

Table 1. Parameter coefficients (± SE) for the general linear models of total body mass (n = 106), fat mass (n = 103), and lean mass (n = 103) for White-throated Sparrows (*Zonotrichia albicollis*) during a stopover at Long Point Ontario during the spring of 2017. Total mass was measured using an electronic mass balance. Fat and lean mass were measured using quantitative magnetic resonance.

Model	Variable (reference level)	β ± SE	F – statistic	p – value
Total mass	Sex (Males)	3.45 ± 0.6	36.65	< 0.0001
	Morph (White-striped)	-0.31 ± 0.30	0.06	0.8
	Age (Adult, ASY)	0.93 ± 0.4	4.57	0.35
	Day of year	0.1 ± 0.03	13.38	0.07
	Time since sunrise	0.004 ± 0.002	2.19	0.005
Fat mass	Sex (Males)	1.60 ± 0.37	19.04	< 0.0001
	Morph (White-striped)	0.04 ± 0.27	0.03	0.87
	Age (Adult, ASY)	0.27 ± 0.28	0.91	0.34
	Day of year	0.14 ± 0.02	47.88	< 0.0001
	Time since sunrise	0.0009 ± 0.001	0.40	0.53
Lean mass	Sex (Males)	1.82 ± 0.29	39.09	< 0.0001
	Morph (White-striped)	-0.01 ± 0.22	0.001	0.95
	Age (Adult, ASY)	0.41 ± 0.22	3.28	0.07
	Day of year	0.0002 ± 0.02	0.001	0.99
	Time since sunrise	0.003 ± 0.001	8.58	0.005

3.3 Stopover refuelling rate

Triglyceride and β-OH butyrate concentrations were measured in 82 birds. Table 2 shows the average CV of each metabolite assay and the measured metabolites concentrations can be found in appendix 3. Three birds were captured in baited ground traps and were excluded from analysis. Triglyceride and β-OH butyrate were negatively correlated ($r = -0.48$, $p < 0.001$), and principal component analysis was applied to generate a refuelling index. Principal component one (PC1) accounted for 74% of the variance, with triglyceride loading positively into PC1 and β-OH butyrate loading negatively. Higher RI values therefore signify higher refuelling rate.

Average bleed time was 6 minutes and 35 seconds, with a standard error of 15 seconds. No correlation was found between bleed time and triglyceride ($r = 0.08$, $p = 0.520$) or β-OH butyrate ($r = 0.06$, $p = 0.652$) in this study, indicating that the time elapsed between capture are blood sampling did not influence the measurement of refuelling rate.

Several birds were either missing data associated with competitor abundance (3), age (7), or QMR data (2), and were excluded from analysis. One bird was excluded as an outlier, likely resulting from low plasma volume. The model of refuelling rate sex, morph, age, fat mass, lean mass, day of year, time since sunrise, and competitor abundance was significant ($F_{8,56} = 2.64$, $p = 0.015$, $R^2 = 0.27$), and was not improved by inclusion of any two-way interactions between factors. RI increased with each minute since sunrise ($F_{1,56} = 8.76$, $p = 0.005$), and was positively associated with fat mass at capture ($F_{1,56} = 4.31$, $p = 0.04$, Table 3). Neither sex nor morph influenced refuelling rate (Figure 7) although females tended to have a higher RI than males ($F_{1,56} = 3.62$, $p = 0.06$). RI also tended to decrease with day of year ($F_{1,56} = 3.19$, $p = 0.07$). The remaining variables did not significantly influence refuelling rate (all $p > 0.2$, Table 3). All model assumptions were satisfied in this analysis.

Table 2. The average ± standard deviation (SD) of the coefficient of variation (CV) for each plasma metabolite assay.

Assay	Average CV ± SD
Glycerol	2.2 ± 2.1
Triglyceride	2.6 ± 2.8
B-OH Butyrate	3.9 ± 3.3

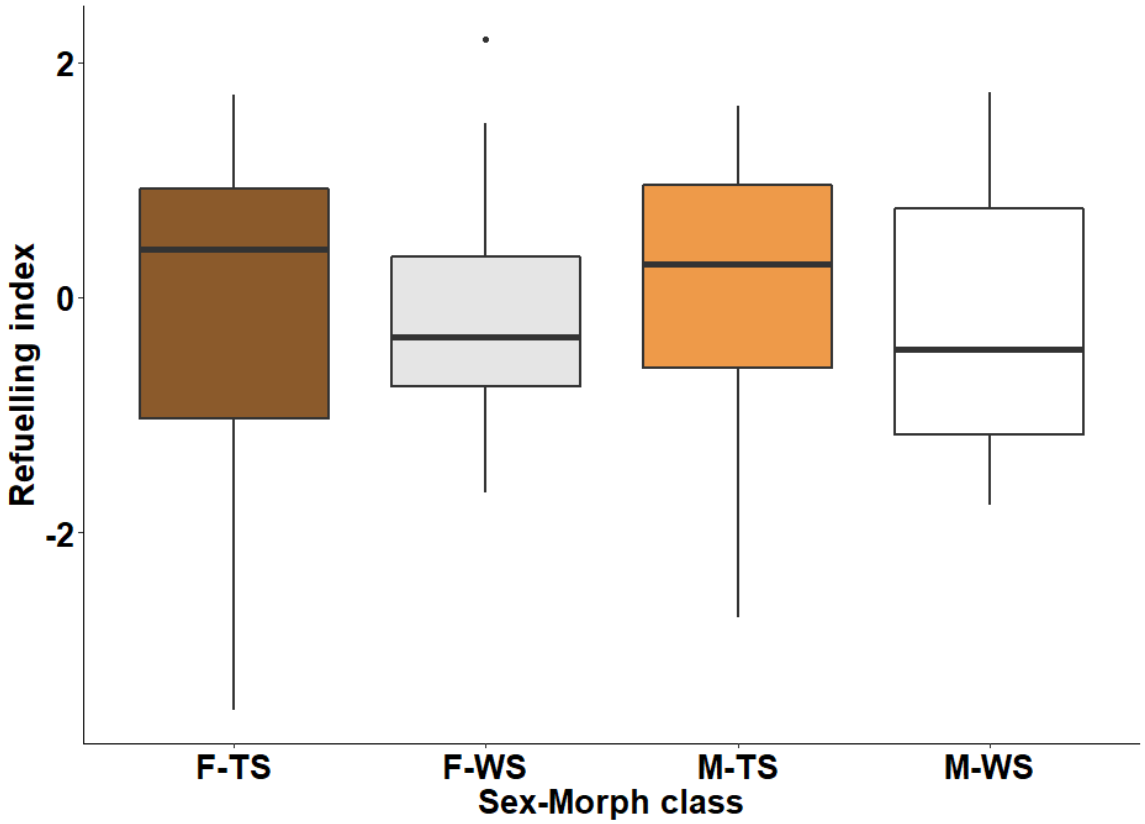

Figure 7. Stopover refuelling index (RI) by sex-morph class for White-throated Sparrows (*Zonotrichia albicollis*) at Long Point, Ontario, Canada, during the spring of 2017. Solid line indicates the median value, with the filled box represents the first and third quartile. Whiskers indicate the minimum and maximum values, and points represent outliers beyond 1.5 * the inter- quartile range.

Table 3. Parameter coefficients (β ± SE) for the general linear model of stopover refuelling rate index (RI) in White-throated Sparrows (*Zonotrichia albicollis*) during a stopover at Long Point Ontario during the spring of 2017.

Variable (reference level)	β ± SE	F – statistic $_{1,56}$	p - value
Sex (Males)	-0.98 ± 0.51	3.62	0.06
Morph (White-striped)	-0.31 ± 0.30	1.02	0.32
Age (Adult, ASY)	-0.34 ± 0.36	0.89	0.35
Fat Mass (g)	0.24 ± 0.12	4.31	0.04
Lean Mass (g)	0.21 ± 0.18	1.43	0.24
Day of year	-0.05 ± 0.03	3.19	0.08
Time since sunrise	0.006 ± 0.002	8.76	0.005
Competitor abundance	-0.0007± 0.004	0.03	> 0.5

3.4 Stopover duration

Temperature and tailwind were significantly positively correlated ($r = 0.41$, $p < 0.001$), and principal component analysis was applied to generate an index of weather condition (see methods). Principal component one (PC1) accounted for 70% of the variance, with both tailwind and temperature loading positively into PC1. Therefore, I interpret PC1 as a weather index representing the favourability of environmental conditions in regard to temperature and tailwind.

I deployed 53 radio tags on White-throated Sparrows during the spring of 2017. Attempts to balance radio tag deployment between the sexes by date were unsuccessful due to site level protandry. Of the 53 radio tagged birds, I was able to confirm the sex of 37, and the morph of 30. Using the sexing criteria from Caldwell and Mills (2006), and assuming the morph assigned in the field is correct, 15 of the remaining 16 birds can be assigned a sex. I believe the assumption of field assigned morph matching genetic morph is valid. Among the radio tagged birds that were successfully morphed using genetics, all matched the field assigned morph. Radio tags were deployed on 22 males and 30 females. Of these, 25 birds were white-striped, and 27 birds were tan-striped (Table 4).

Stopover duration ranged from 1- 23 days (median of 7 days) with all birds departing before 21 May 2017. In the Cox proportional hazard model of stopover duration, the hazard for departure was influenced primarily by the weather index, and by day of year, and was unaffected by sex (Figure 8), morph (Figure 9), fat mass, lean mass, and competitor abundance (Table 5). After controlling for covariates, the hazard for departure increased by 117% for each unit of tailwind and temperature, and 8.5% for each day of year.

Table 4. Average stopover duration ± standard error at Long Point, Ontario for each White-throated Sparrow sex-morph class during the spring of 2017.

Sex-morph class	N	Stopover duration (days) ± standard error
White-striped male	11	8.8 ± 2
White-striped female	14	9.3 ± 1.4
Tan-striped male	11	5.5 ± 1.4
Tan-striped female	16	7.3 ± 1.4

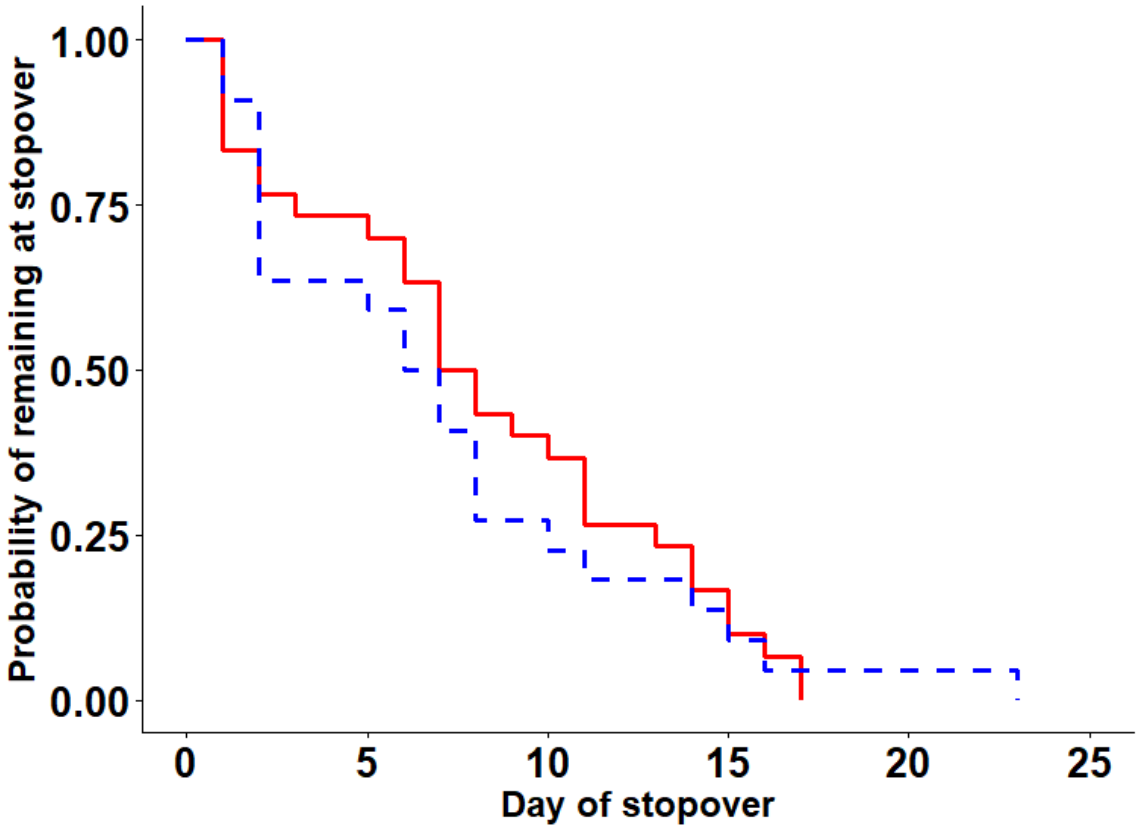

Figure 8. Kaplan-Meier survival estimates showing the probability of remaining at stopover at Long Point, Ontario, Canada for White-throated Sparrows (*Zonotrichia albicollis*) during the spring of 2017. Males (N= 22) are represented by the dashed line, and females (N= 30) are represented by the solid line.

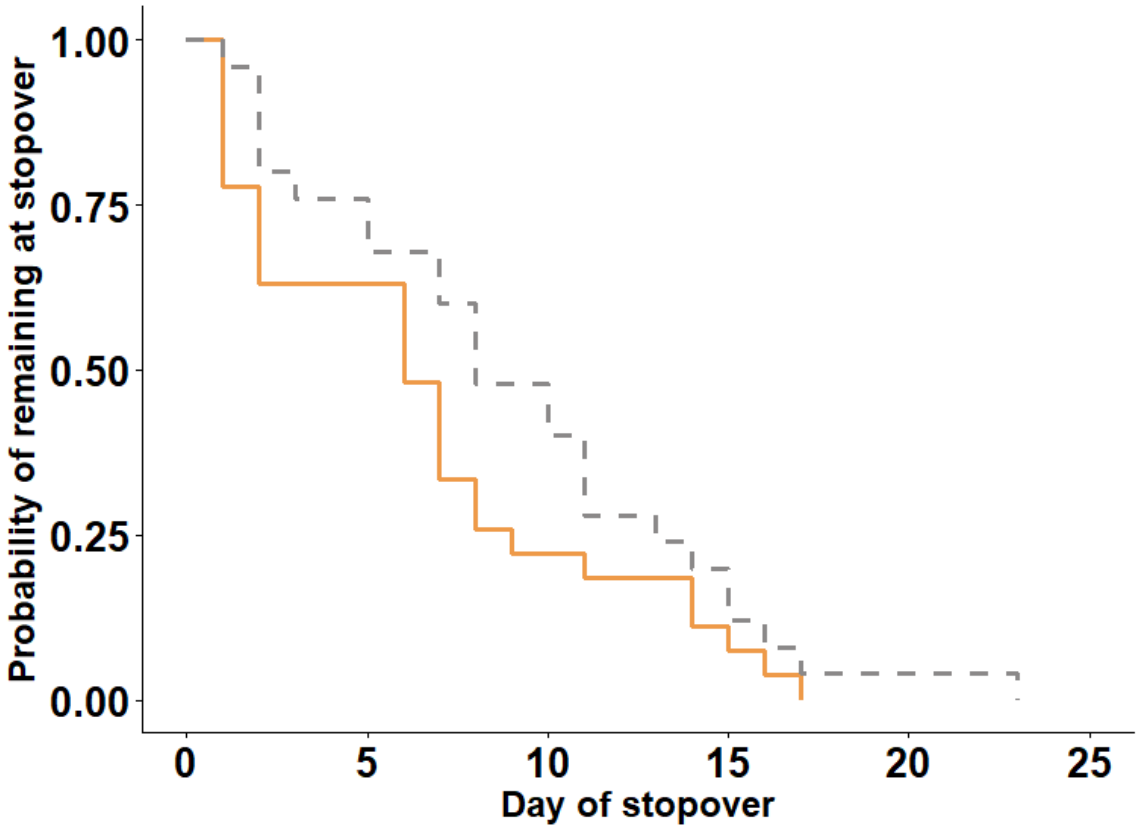

Figure 9. Kaplan-Meier survival estimates showing the probability of remaining at stopover at Long Point, Ontario, Canada for White-throated Sparrows (*Zonotrichia albicollis*) during the spring of 2017. Tan-striped birds (N= 25) are represented by the solid line, and white-striped birds (N= 27) are represented by the dashed line.

Table 5. Parameter coefficients (± SE) of the Cox regression model of stopover duration in White-throated Sparrows during a stopover at Long Point, Ontario, during the spring of 2017. Also shown are the chi-squared values, p-values, and hazard ratios (HR).

Variable	β ± SE	Chi-square	p-value	HR
Sex (Females)	-0.73 ± 0.60	1.51	0.22	0.49
Morph (Tan-striped)	0.36 ± 0.32	1.23	0.26	1.43
Fat Mass (g)	0.24 ± 0.14	2.90	0.09	1.27
Lean Mass (g)	0.19 ± 0.17	0.93	0.33	1.18
Day of year	0.08 ± 0.04	5.35	0.02	1.09
Weather index (PC1)	0.77 ± 0.16	23.11	<0.001	2.17
Competitor abundance	-0.003 ± 0.004	0.52	0.47	0.99

3.5 Wintering latitude

Head feather δ^2H values were compared for 64 birds using a general linear model. Age was omitted from the model as several morph-sex-age classes had less than 6 individuals, and because the differences between sex and morph classes were of primary concern. A likelihood ratio test indicated that the inclusion of a sex by morph interaction improved model fit. Despite this, the model of head feather δ^2H values containing sex, morph, and a sex by morph interaction was not significant ($F_{3,60} = 1.49$, $p = 0.23$). Head feather δ^2H values did not differ between sex ($F_{1,60} = 3.03$, $p = 0.09$) or morph ($F_{1,63} = 0.90$, $p = 0.35$) classes, and the sex by morph interaction was not significant ($p = 0.61$). Males tended to have a more negative δ^2H_f value than females indicating a more northern wintering latitude. This pattern is generally reflected in the maps of likely origin, with a greater proportion of males and adults assigned to the northern part of the wintering range (Figure 10). All model assumptions were satisfied in this analysis.

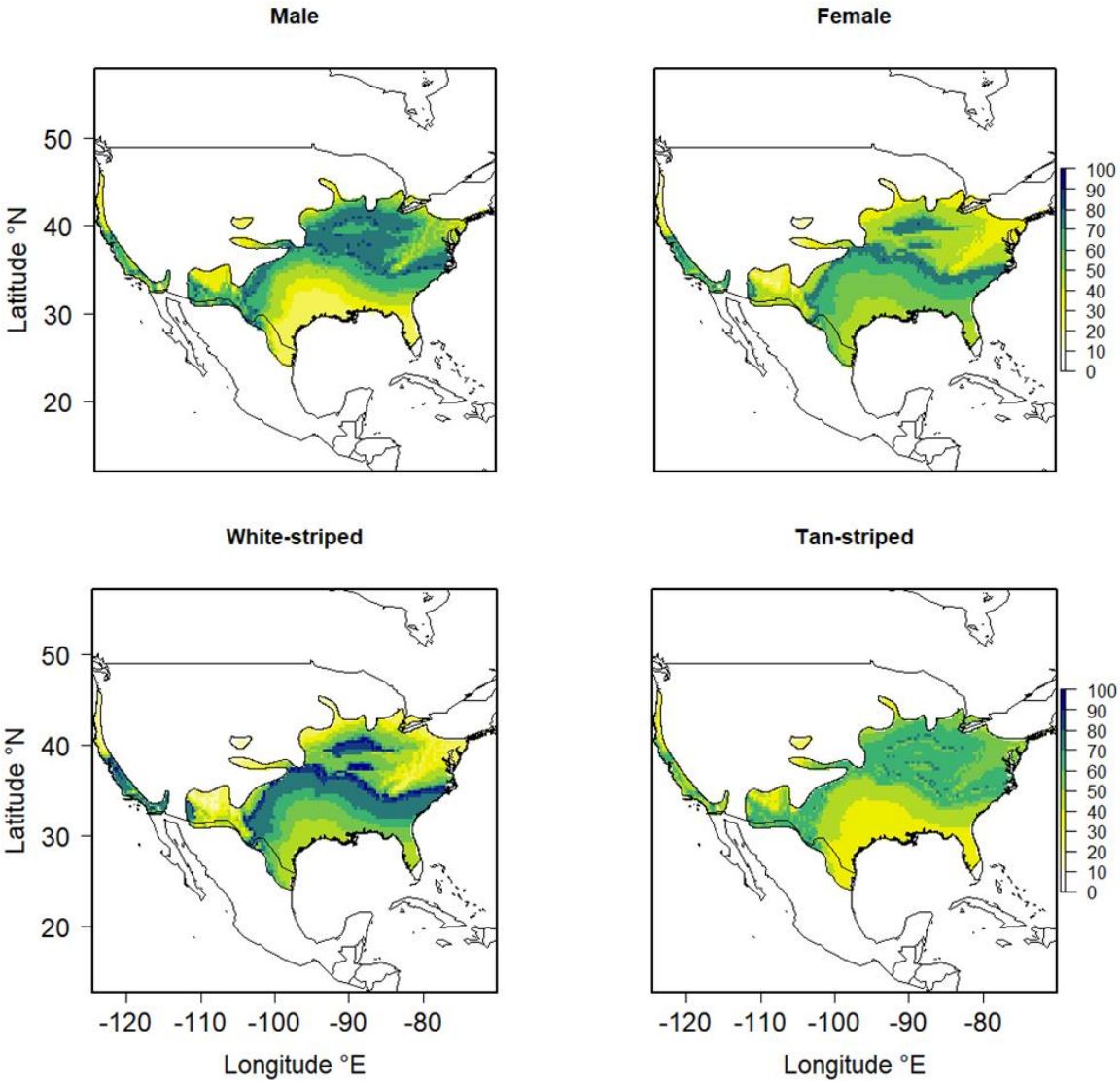

Figure 10. The geographic distribution of assigned wintering location for White-throated Sparrows (N=64) sampled at Long Point, Ontario, Canada, during the spring of 2017. Assignments are based on a likelihood-based comparison between head feather isotopes values and predicted isoscape from Bowen et al. (2005). Colour represent the proportion of individual in the sex or morph class that can be assigned to each cell in the raster isoscape, with darker colour representing a higher proportion of that class being assigned to that region.

Discussion

Differential migration timing is commonly observed in songbirds, however, the underlying mechanisms are still uncertain for many species. Three key behavioural mechanisms thought to influence migration timing are migration speed, migration distance, and migration initiation date (Coppack and Pulido 2009). In this thesis, I examined aspects of migratory stopover ecology pertaining to migration speed, and migration distance between the sexes, morphs, and age classes of the White-throated Sparrow using a suite of advanced techniques. Plasma metabolite analysis and automated radio telemetry were used to measure stopover refuelling rate and stopover duration; two aspects of migration ecology believed to influence migration speed. Migration distance was inferred using stable isotope analysis. Because protandry is known to occur in the White-throated Sparrow, I tested the hypothesis that males would have a higher stopover refuelling rate and shorter stopover duration than females. This could theoretically contribute to a faster overall migration speed in males compared to females as less time would be spent at stopover sites during migration. I also expected males to overwinter at more northern latitudes, indicating a shorter overall migration distance. Morph-specific migration timing has been observed in the White-throated Sparrow (Knapton et al. 1984, Caldwell and Mills 2006, Mazerolle and Hobson 2007), however, little is known about morph-specific spring stopover ecology. Behavioural traits exhibited by white-striped birds may influence resource competition at stopover, and so I expected white-striped birds to refuel faster, and depart stopover sooner. I also tested for morph specific wintering latitude.

4.1 Migration timing

White-throated Sparrows showed significant protandry in their arrival date at Old Cut, with males arriving around 11 days earlier than females. There was no discernable difference in the arrival date between morphs. The degree of protandry is similar to the findings of Mills (2005), who found that males arrive around 10 days earlier than females using a 24-year LPBO banding dataset. White-throated Sparrows migrating through Long Point exhibit a degree of protandry slightly higher than the seven days reported for

White-throated Sparrows migrating through the Delta Marsh Bird Observatory (Mazerolle and Hobson 2007), and could represent a population difference between birds breeding in Ontario and Manitoba. The degree of protandry exhibited by White-throated Sparrows appears to be high relative to many other migratory songbird species. Among 18 wood warbler species captured during migratory stopover at Prince Edward Point, Ontario, protandry values ranged from two to five days (Francis and Cooke 1986). Examining a multi-decadal banding dataset of 30 protandrous North American songbird species, Kissner et al. (2003) found that protandry ranged from 0.5 to 12.7 days, with an average protandry value of five days. Among eight common migratory European songbirds species, Tøttrup and Thorup (2008) found an average degree of protandry of only three days.

Higher degrees of protandry are expected when operational sex ratios are male-biased, and there are high levels of extra-pair mating (Kokko et al. 2006). Past studies focusing on White-throated Sparrows migrating through Long Point have found a male bias in sex ratios (Mills 2005), suggesting that access to females may be limited during the breeding season. Extra-pair mating is also known to occur in the White-throated Sparrow, although mainly between white-striped males and tan-striped females (Tuttle 2003). Around 30% of the nestlings in white-striped male and tan-striped female nests were the result of an extra pair fertilization, compared to only 4.4% of nestlings in tan-striped male and white-striped female nests (Tuttle 2003). White-striped males appear to employ a reproductive strategy focused on maximising fitness through extra-pair copulations (EPC), whereas tan-striped males focus on maximising fitness through mate guarding (Tuttle 2003, Falls and Kopachena 2010). If the level of EPC differs between the sex-morph pairings, why is there no major difference in the degree of protandry exhibited by each sex-morph pair? With greater rates of EPC, the protandry exhibited in the white-striped male and tan-striped female pairings should theoretically be greater. Hypothetically, this could manifest as the earlier arrival of white-striped birds, either exclusively in males or within each sex. Differences in arrival timing between morphs was reported by Mazerolle and Hobson (2007) for White-throated Sparrows migrating through the Delta Marsh Bird Observatory, with white-striped birds arriving around 4.8 days earlier than tan-striped birds. However, other studies have reported only a slight

difference in migration timing between morphs, both at stopover sites and on the breeding grounds. At breeding areas in Algonquin Provincial Park, Knapton et al. (1984) compared the distribution of arrival dates for each morph within each sex, and found that white-striped birds arrived slightly earlier, but the difference between morphs was only significant within females.

Caldwell and Mills (2006) found morph-specific arrival timing in White-throated Sparrows using banding data collected by the LPBO, with white-stiped birds arrive around two days earlier than tan-striped birds. Further examining morph specific migration timing within each sex, Caldwell and Mills (2006) found a significant difference within females, with white-striped birds arriving around 1.3 days earlier than tan-stiped birds. These studies suggest that the protandry between tan-striped males and white-striped females may be lower than white-striped male and tan-striped female pairings, however, these reported differences are small compared to the overall degree of protandry exhibited by both sex-morph pairings of the White-throated Sparrow. One possible explanation is that both the mate guarding strategy of the tan-striped male and the EPC strategy of the white-striped males have benefits associated with early arrival. For example, Møller et al. (2008) observed higher rates of extra-pair young in the nest of late arriving male Barn Swallows. Another potential explanation is that the selection for earlier male arrival resulting from the reproductive strategy of the white-striped male results in earlier arrival timing in males of both morphs. Perhaps the genetic mechanism underlying the mating strategy is morph-specific, but the selective pressures associated with the mating strategy of the white-striped male acts on the traits associated with earlier migration in males of both morphs.

I did not observe any difference in first capture timing between ages. Age-specific migration schedules are known to occur among many migratory songbirds (Francis and Cooke 1986, Stewart et al. 2002). Stewart et al. (2002) examined age-specific spring migration timing using a 14-year LPBO banding dataset. Comparing age-specific migration within each sex, adult males migrated significantly earlier than juvenile males in 16 of 20 species examined, and adult females migrated significantly earlier than juvenile females in 8 of 12 species examined; adults preceded juveniles by 2-3 days.

White-throated Sparrows, nor any other sparrow species, were not included in their study. Juveniles might be at a disadvantage when competing for territories due to their lower competitive ability or social dominance (Sherry and Holmes 1989), suggesting that their optimal arrival date on the breeding grounds might be later than adults (Kokko et al. 2006). In overwintering flocks, juvenile White-throated Sparrows are generally sub-dominant to adults (Piper and Wiley 1989), however, it is unclear if this pattern holds true during migration.

4.2 Stopover refuelling rate

My study adds to the mounting evidence suggesting that sex classes can refuel equally well, and that differential stopover refuelling ability is not a general mechanism that contributes to protandry in migratory songbirds. While not significant, the refuelling rate model indicated a tendency for females to have a higher refuelling than males, strongly suggesting that differences in refuelling rate do not underlie the migratory protandry observed in White-throated Sparrows. Past studies have provided mixed conclusions regrading how sex differences in stopover refuelling rate contribute to migratory protandry across multiple avian taxa. In Seewagen et al. (2013), sex-specific refuelling rates were found in two protandrous warbler species during spring migration stopover bouts in parks surrounding the New York Metropolitan area. Schmaljohann et al. (2016) found that male Northern Wheatears (*Oenanthe oenanthe*) of the *leucorhoa* subspecies refuelled faster than females, and, using modelling, predicted that the difference in refuelling rate would result in a degree of protandry near observed values. Other studies have failed to find an effect of sex on refuelling rate (Morris et al. 2003, Smith et al. 2007, Macdade et al. 2011, Hays et al. 2018, Morbey et al. 2018), suggesting that sex-specific stopover refuelling rate is not an important contributor to protandry.

I observed no effect of morph on refuelling rate, suggesting that behavioural differences known to exist between the morphs do not influence stopover refuelling during spring stopover at Long Point. This finding contradicts the pattern found in fall migrating White-throated Sparrows, where white-striped birds had a higher stopover refuelling index than tan-striped birds (Brown et al. 2014). Seasonal differences in behaviour and physiology may explain why morph influenced refuelling rate during

stopover in the fall but not during spring. Higher refuelling rates have been observed during the spring in some songbird species (Seewagen et al. 2013). One possible explanation for the absence of morph-specific refuelling rate during the spring is that any intrinsic changes associated with increased spring refuelling rate may not occur evenly in white-striped and tan-striped birds. Tan-striped birds may have a considerably higher refuelling rate in the spring, whereas the spring and fall refuelling rate of white-striped birds may be comparable. Comparison of spring and fall refuelling rate in captivity may provide some insight into this question.

Age-specific stopover refuelling rate is generally not observed in spring migrating songbirds, and the findings of my study concurs with this pattern (Morris et al. 2003, Seewagen et al. 2013, Morbey et al. 2018). Behavioural differences related to competitive ability, social status, foraging skills, and physiological differences regarding the digestive system have been suggested to influence refuelling ability (Woodrey 2000, Moore et al. 2003, Stein et al. 2005). These differences are likely greatest in the fall, when juvenile birds are migrating for the first time. Given that Brown et al. (2014) found no effect of age on stopover refuelling rate in fall migrating White-throated Sparrows, it is not surprising that no effect of age was found in the spring.

One possible explanation for the absence of an effect of sex, morph, and age on refuelling rate is that food resources are not limited during spring stopover at Old Cut, potentially reducing the amount of intraspecific competition for resources, or reducing the negative impact of resource competition on refuelling rate below a detectable level. During the fall when resources are less abundant, competition for scarce resources may have a greater impact on refuelling rate, contributing to the morph-specific refuelling rate found by Brown et al. (2014). Although I did not specifically examine resource abundance at Old Cut, greater food availably and higher refuelling rates in the spring compared to the fall has been reported at other sites. Smith (2013) found a non-significant trend for White-throated Sparrows to have a higher refuelling rate in the spring compared to the fall at the Braddock Bay Bird Observatory (Hilton, NY, USA). Although not specifically examined, Seewagen et al. (2011) reported higher leaf litter invertebrate biomass during the spring than in the fall at several stopover sites

surrounding New York City (NY, USA). Behaviourally based differences in stopover refuelling rate may then have some aspect of site quality dependence, with poorer competitors having a lower refuelling rate when food resources are scarce. Examining the occurrence of class-specific refuelling rate between sites of varying quality, perhaps under controlled conditions, may provide further insight into this question.

Stopover refuelling rate was significantly influenced by fat mass at capture, and the time elapsed since sunrise. Previous studies examining refuelling rate using plasma metabolite analysis have found an effect of condition or mass on refuelling, with greater condition and mass positively influencing metabolite concentrations (Schaub and Jenni 2001, Guglielmo et al. 2002, Macdade et al. 2011, Smith 2013). There are several possible explanations for this finding. Birds with higher fat mass may be in a higher energetic condition, enabling more efficient foraging and refuelling. Alternatively, birds with a higher refuelling rate may be less likely to be captured with low fat mass. To ensure that the relationship between fat mass and refuelling rate was not biasing the RI model, I removed the fat mass, and re-examined the influence of the remaining variables. The direction and significance of the remaining effects were unchanged. Time of day also significantly influenced refuelling. A gradual increase in refuelling index throughout the day is likely the result of the turnover in metabolite profile from an overnight fasting to a daytime refuelling state, and has been observed in multiple studies (Guglielmo et al. 2005, Seewagen et al. 2011, 2013; Brown et al. 2014, Morbey et al. 2018). A potential confounding factor related to studying granivorous White-throated Sparrows at Old Cut is the use of bird feeders and baited ground traps. The artificial supplementation of food in and around the Old Cut banding station could theoretically affect refuelling rate and overall stopover duration. One direct consequence of this would be a higher refuelling rate observed in birds captured shortly after feeding at or around bird feeders and baited ground traps.

If the primary mechanism underlying sex or age differences in refuelling rate is competitive ability, with better competitors securing more resources and thus refuelling faster, high food availability could potentially reduce the observable contrast between individuals. Additionally, the consequences of being a less competitive individual might

be negated when resources are highly abundant, as another patch with high food availability is readily available. Supporting this notion, White-throated Sparrows were often observed feeding at baited ground traps and bird feeders located throughout the Old Cut banding stations.

4.3 Stopover duration

Stopover duration did not differ between males and females, nor between white-striped or tan-striped birds. This finding is unsurprising given that neither sexes nor morphs differed in stopover refuelling rate. Despite the clear evidence of protandry in the White-throated Sparrow, the similarity in stopover duration between sexes may suggest that the overall speed of migration does not differ, however, additional information about other aspects contributing to migration speed is required before drawing further conclusions. Differences in flight speed and the frequency of stopover bouts could also contribute to differences in overall migration speed. For instance, additional stopover bouts conducted by females White-throated Sparrows prior to arrival at Long Point could both explain the later arrival of female observed in this study, and the pattern of protandrous breeding ground arrival timing observed previously in this species. Interestingly, the similarity in stopover duration between sex and morph classes may suggest that other costs associated with stopover, such as searching and settling costs, may not differ between sex and morph classes. Prolonged time required for finding a suitable stopover location prior to refuelling may increase overall stopover duration. For example, if female White-throated Sparrows expend more energy or time searching and competing for a stopover patch prior to refuelling, this could theoretically result in an increased stopover duration (Alerstam and Lindström 1990).

Higher average daily temperatures and greater tailwind assistance significantly increased the risk of departure. Evidence suggests that temperature can act as a direct departure cue for departure from stopover (Newton 2008, Metcalfe et al. 2013, Berchtold et al. 2017). Metcalfe et al. (2013) examined the effects of inclement weather on the nocturnal migratory restlessness of captive White-throated Sparrows during spring by manipulating barometric pressure and temperature. A decrease in migratory restlessness was observed following a decrease in temperature combined with an increasing pressure,

however, increased temperature and decreased pressure did not produce a corresponding increase in migratory restlessness over the unmanipulated control. The control temperature in Metcalfe et al. (2013) was 19° C, whereas the average daily temperature I recorded over the course of my study was 11° C. The control condition in Metcalfe et al. (2013) may correspond to favourable migratory conditions in a natural setting. This could explain why increasing temperature and decreasing pressure did not increase migratory restlessness compared to controls.

During spring migration, warmer temperature may be associated with southerly tail winds. Many studies have demonstrated a correlation between favourable tailwinds and migratory behaviour (Erni et al. 2002, Eikenaar and Schmaljohann 2014, Dossman et al. 2016, Morbey et al. 2018). This behaviour likely reduces the cost per distance flown, and the amount of correction required for crosswind drift (Alerstam and Lindström 1990, Liechti 2006), and may positively influence both survival and productivity (Drake et al. 2014). It is likely that both temperature and tailwind are important factors governing the decision to migrate, with rising temperature acting as an initial cue to initiate migration, with final departure decisions made after wind conditions have been assessed aloft. While there was a tendency for fat mass to increase departure risk, this effect was not significant. It is important to note that fat mass was measured at capture, and this may not correspond to departure fat mass. The effect of temperature, tailwind, and fat mass might suggest that the decision to depart from stopover follows a hierarchical process. Birds in good condition might be cued to migrate by warmer daily temperatures, with the final departure decision made after wind conditions have been assessed once airborne. A hierarchical departure decision process might help to explain the extended diel activity on departure nights observed in White-throated Sparrows, Magnolia Warblers (*Setophaga magnolia*), and Black-throated Blue Warblers (*Setophaga caerulescens*) by Morbey and Beauchamp (In review). We found later evening activity on departure nights relative to the previous night. Although the purpose of delayed quiescence is uncertain, it suggests that the decision to depart was made prior to the time when birds would cease normal diurnal activity. Temperature cues throughout the day of departure may prime birds to continue migration, producing this later activity.

Finally, day of year slightly but significantly increased departure risk, suggesting that later arriving birds had a shorter stopover duration. Shorter stopover duration later in the season may be a strategy employed by later migrating birds to “catch-up”. Favourable environmental conditions later in the migratory season may also contribute to this phenomenon, although this effect would have been achieved independently of stopover refuelling rate, as date did not influence refuelling. Perhaps reduced overnight thermoregulatory cost with warmer late season temperatures enable a larger net gain in energy storage per stopover day.

4.4 Wintering latitude

Overwintering at more northern latitudes has the potential to contribute to earlier arrival on the breeding grounds, as less distance needs to be traversed during the migratory season. I examined wintering latitude by conducting stable hydrogen isotope analysis on the head feathers. I found no significant effect of sex or morph on head feather δ^2H values suggesting that there was little difference in wintering latitude between sex or morph classes. Past studies based on banding and museum specimens have found a latitudinal cline in winter sex ratios in the White-throated Sparrow (Jenkins and Cristol 2002). Perhaps a gradual decrease in the proportions of males with decreasing wintering latitude does not translate into a statistically significant difference in head feathers δ^2H values which are also inherently variable. A significant sex effect was observed by Mazerolle and Hobson (2007), who found that male head feather δ^2H values were more isotopically negative, indicating a more northerly wintering latitude. One potential explanation for the discrepancy between this study and my own is that the birds migrating through Delta Marsh and Long Point may belong to different sub-populations of White-throated Sparrows, and the population passing through Long Point may exhibit a lower degree of latitudinal sex segregation on the wintering grounds. Methodological differences in the assignment of sex between my study and previous studies may have also contributed to the discrepancy between my results and the results of previous studies. All birds included in my analysis were sexed using genetics, whereas Mazerolle and Hobson (2007) and Jenkins and Cristol (2002) relied on a measure of wing chord to assign sex. While these methods are can have and accuracy greater than 90% (Piper and

Wiley 1991), the use of genetics in my study to confirm sex prevented the exclusion or misclassification of individuals with intermediate wing lengths. Including intermediately sized individuals may have reduced the differences between males and females. Finally, my findings are based on a single year of data from a comparatively small number of individuals, inter-year variability in conditions on the wintering ground and sample size difference between my study and previous studies may have also contributed to the discrepancy between my findings and the findings of previous studies. Given that male White-throated Sparrows arrived at stopover significantly earlier than females, my finding of minimal difference in wintering latitude between the sexes suggests that differences in migration distance in relation to wintering latitude do not greatly influence arrival timing at breeding areas. No effect of morph was found on wintering latitude, echoing the findings of Mazerolle and Hobson (2007). My finding adds further evidence that latitudinal stratification by morph, mediated by behavioural or other morph related differences, does not appear to occur in the White-throated Sparrow.

4.5 Assumptions and limitations

Several assumptions were made during this study. Like most studies, I assumed that the birds I sampled are representative of the White-throated Sparrow population, or that all birds come from populations that exhibit similar patterns of migration timing. As sparrows were blood sampled opportunistically, I do not believe any sampling bias was introduced. I attempted to balance the birds selected for radio tagging by sex, morph, and date to reduce any effect of date on stopover duration. By recording the number of birds tagged in each sex-morph cohort, I could determine which group needed individuals to be tagged on a given day. By tagging the first White-throated Sparrow that fit this criterion, I do not believe any sampling bias was introduced. One critical assumption related to the measurement of stopover duration is that birds were captured near the beginning of their stopover bout. Because the true arrival date of each bird is unknown, the measured stopover duration is a conservative estimate of the true stopover duration.

This study was limited to one year of data collection, and as a result, generalising the findings of this study requires the assumption that the migration season of 2017 represented a typical migration season. The spring of 2017 had several high rainfall

events which may have influenced stopover behaviour. Years with less rainfall may have improved migratory conditions, which could potentially influence stopover duration.

4.6 Future directions

The findings of my study indicate that stopover refuelling rate and stopover duration does not contribute to the protandry observed in the White-throated Sparrow. Future studies attempting to determine the underlying mechanisms of migration timing should focus on other aspects of sparrow migration ecology. One aspect that should be focused on in particular is migration initiation timing. Initiating migration at an earlier date would promote protandry without requiring males to have shorter stopover durations, higher refuelling rates, or drastically shorter migration distances. Odum (1949) found that male White-throated Sparrows departed wintering areas two weeks earlier than females. Sexing was conducted via dissection on lethally collected birds, and using a combination of wing chord and plumage colouration on non-lethally trapped birds. However, one issue with this study is that the plumage dimorphism exhibited by the White-throated Sparrow had yet to be recognized at the time and was not expressly examined. This may have confounded their determination of sex. Odum (1949) also noted that birds lingering on the wintering grounds later in the season were “dull plumaged”, suggesting that these may have been tan-striped birds. Given our current understanding of the White-throated Sparrow’s plumage dimorphism, and our ability to use genetics to confirm sex and morph, differential migration initiation timing should be re-evaluated.

Other studies have suggested that migration initiation date is an important mechanisms of differential migration timing in other species. Using light level geolocators, McKinnon et al. (2014, 2016) found that the later departure from overwintering areas contributed to later arrival at breeding areas in juvenile Wood Thrush and female Snow Bunting (*Plectrophenax nivalis*). Examining winter and early spring banding data, Catry et al. (2005) found that in protandrous Common Chiffchaffs (*Phylloscopus collybita*), males departed African overwintering areas earlier than females. Additionally, several studies that have examined migratory restlessness in protandrous species as an indicator of migration initiation timing have found that onset of

migratory restlessness occurs at an earlier date in males than in females (Terrill and Berthold 1990, Coppack and Pulido 2009, Maggini and Bairlein 2012).

In addition to examining migration initiation timing, future studies should also examine if there is a relationship between social dominance, late winter body condition, and migration initiation timing in the White-throated Sparrow. Cristol et al. (2014) found that male White-throated Sparrows supplemented with food in late winter moulted earlier and initiated spring migration at an earlier date than non-supplemented birds. Access to food resources during winter is influenced by social dominance in White-throated Sparrows (Piper and Wiley 1990), and this could result in subordinate birds initiating migration later. A similar phenomenon is believed to occur in American Redstarts (Marra et al. 1998). This could contribute to differential departure timing from the wintering grounds in the spring. An interaction between late winter dominance status, late season environmental conditions, and migration initiation timing might also contribute to the slight effect of morph I observed on migration timing. In years with harsh late-winter conditions, a cascading interaction between food availability, social dominance, food access, moult timing, and the start date of migration might result in males and white-striped birds initiating migration earlier than females and tan-striped birds. This cascade may not occur in years with favourable late season conditions, and may explain why I did not observe morph-specific migration timing.

Another aspect of migration ecology that warrants further investigation is the frequency of stopover bouts. Male White-throated Sparrows may be conducting fewer stopover bouts during the course of migration compared to females, and this could contribute to differential breeding ground arrival timing (McKinnon et al. 2014). Differences in wing morphology may influence flight energetics, allowing males to fly a greater distance on a given fuel load. Males may also depart stopover with a higher fuel load enabling longer flight bouts and reducing the number of stopovers required to reach the breeding grounds. Information on departure fuel load may help to clarify this question. Further development of the Motus Wildlife Tracking System, or global positioning system telemetry,

could allow us to track the migration of White-throated Sparrows over the duration of the entire migratory season. With this information, flight distance, stopover frequency, stopover duration, and migration distance could be examined concurrently. The rate of energy use during sustained flight could also be measured in captive White-throated Sparrows using a wind tunnel to determine if flight energetics differ among sex, morph, and age classes.

Repeating this study, both at Old Cut and at different sites would provide a variety of benefits. Repeating this study at Old Cut would test if foraging conditions during the spring of 2017 may have buffered sex differences in refuelling. Replicating this study at different sites would allow for an examination of site quality. I feel this is particularly important given the potential confounding effect of bird feeders and baited ground traps used in and around the Old Cut banding station. Replicating this study in a site with no artificial food sources available might yield a different pattern of sex, morph, or age-specific stopover behaviour. Removal of artificial food sources could increase competition for the remaining food sources available. This may accentuate differences in refuelling between individuals of differing competitive ability, revealing patterns of sex, morph, or age specific refuelling that are not present when food resources are plentiful. In turn, stopover duration could also be influenced via the relationship between refuelling rate and stopover duration. Assessment of food availability and habitat quality could also be incorporated during a replication of this study. Direct measurement of both refuelling rate and stopover duration on the same individual might help to further clarify the interdependence of departure decisions on stopover refuelling rate in White-throated Sparrows.

Additionally, this study could be repeated during the fall. This would test if the findings of Brown et al. (2014) are repeatable between years. Another benefit would be the chance to examine the relationship between stopover duration and refuelling rate between groups known to differ in stopover refuelling rate. White-striped birds would be expected to have a shorter stopover duration in relation to their known higher refuelling rate.

4.7 Conclusions

Differential migration timing is commonly observed in spring-migrating songbirds. Despite the ubiquity of differential migration, uncertainty still exists about the behavioural mechanisms that underlie this pattern. The intriguing plumage dimorphism exhibited by the White-throated Sparrow provided an opportunity to examine how behaviour influences migration ecology beyond sex and age. The findings of my study suggest that the high degree of protandry observed in spring White-throated Sparrow migration is unrelated to sex-specific stopover behaviours, corroborating well with the conclusions of other studies of protandrous songbird species. My results indicate that migration speed may not differ between males and females, although additional study on the other aspects of migration speed (e.g. flight speed and stopover frequency) is required before further conclusions can be made. In this study, I found no support for sex-differences in wintering latitude as a behaviour underlying the high degree of protandry observed. Of the three behavioural mechanism of migration timing suggested by Coppack and Pulido (2009), my findings suggest that differential initiation of migration may have a greater contribution to sex-specific migration timing. The well-documented behavioural differences between morphs did not appear to influence any of the aspects of migration that I studied, suggesting that the differences in aggression and dominance do not directly translate into differences in migratory behaviour. Morph did not influence refuelling rate or stopover duration, indicating that individual behaviours related to competitive ability may not affect stopover behaviour. However, I believe that the influence of site quality should be considered before drawing further conclusions regarding this. Finally, my study further corroborates the role of environmental variables such as wind and temperature as important factors governing stopover departure decisions in migratory birds.

The influence of extrinsic factors on stopover refuelling rate and stopover duration may reduce or prevent the selection for differential stopover behaviour as a behavioural mechanism to achieve differential migration timing. Variability in environmental conditions and stopover site quality, both within and among years, could influence both refuelling rate and stopover duration, resulting in a high variability in overall migration speed. This could yield a highly variable degree of differential

migration timing. For example, poor conditions may prevent males from refuelling faster or departing stopover sites earlier than females, resulting in equal migration speed and reducing the degree of protandry. Differences in stopover site use between individuals in the same population may cause additional extrinsic variability in overall migration speed. If subsets of a breeding population use different stopover sites of differing quality, variability in the stopover site quality may have a larger influence on refuelling rate than intrinsic differences in refuelling ability. Together, this may prevent consistent selection for faster refuelling on an individual level. Furthermore, a behavioural adaptation for shorter stopover durations could result in negative consequences if departure occurs before adequate refuelling or during unfavourable migratory conditions. Migration initiation date may be less susceptible to extrinsic factors, resulting in greater stability in the differential migration timing achievable through these behavioural mechanisms. Likewise, migration distance may depend more on individual decisions about where to cease migration in the fall, and may be less affected by short term environmental conditions. This may permit stable directional selection to act on migration initiation date and migration distance to produce migratory protandry.

Migration is a fundamental behavioural component of the life history of many North American songbird species. Optimal migration timing can have profound impacts on population health and viability (Visser et al. 2004, Both et al. 2006), and the relationship between breeding ground arrival timing, courting, nesting, and the provisioning of young is likely adapted to best capitalise on ephemeral resource abundances. In the era of climate change, a robust understanding of avian migration will help us to better predict how birds may adaptively respond to the changes in resource phenology predicted to occur (Charmantier et al. 2008). Additionally, if migratory species are detrimentally affected by climate change, improved knowledge of migration may better inform conservation strategies to protect and conserve vulnerable bird populations during their migratory journeys.

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Appendices

Appendix 1a. University of Western Ontario, Council on Animal Care, Animal Use Protocol 2010-020. Issued to Christopher Guglielmo.

Chris Guglielmo

From: [redacted]
Sent: March-28-14 12:36 PM
To: [redacted]
Cc:
Subject: eSirius Notification - New Animal Use Protocol is APPROVED2010-020::5

AUP Number: 2010-020
PI Name: Guglielmo, Christopher
AUP Title: Physiological Ecology Of Migratory Birds And Bats

Approval Date: 03/28/2014

Official Notice of Animal Use Subcommittee (AUS) Approval: Your new Animal Use Protocol (AUP) entitled "Physiological Ecology Of Migratory Birds And Bats

" has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal.2010-020::5

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Copeman, Laura
on behalf of the Animal Use Subcommittee
University Council on Animal Care

1

Appendix 1b. Environment Canada scientific capture permit 10169 BU, issued to Christopher Guglielmo.

Environment Canada / Environnement Canada
Canadian Wildlife Service / Service canadien de la faune

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires
Ontario

Permit No. / N° de permis: **10169 BU**

Issued under the Migratory Birds Regulations Sections 4 and 19.

If the authorizations include any species that are not protected under the Migratory Bird Convention Act, 1994, this document represents an agreement between Environment Canada and the holder for the use of federal bird bands on those species. All conditions listed on the back of this document apply.

Émis en vertu des articles 4 et 19 des règlements concernant les oiseaux migrateurs.

Si les autorisations visent des espèces qui ne sont pas protégées en vertu de la Loi de 1994 sur la convention concernant les oiseaux migrateurs, le présent document tient lieu d'entente entre Environnement Canada et le titulaire aux fins de l'utilisation de bagues fédérales sur ces espèces d'oiseaux. Toutes les conditions figurant au verso du présent document s'appliquent.

Name and Address - Nom et adresse
CHRISTOPHER GUGLIELMO
DEPT OF BIOLOGY
[redacted]

Issue Date / Date d'émission: 2017/04/12

Expiration Date / Date d'expiration: 2017/12/31

Signature of Holder - Signature du détenteur

For the Minister - Pour le Ministre
Name (Print) - Nom (Lettres moulées)
L. LAURIN

Signature [redacted]

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band passerines and other landbirds
- Take, possess, and transport feather samples (1 rectrix and 2-3 head feathers) from WTSP on up to 60 birds (IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL)
- Take, possess, transport other biological samples (<1.5mm claw clip from central claws on each foot) from WTSP on up to 260 birds (includes claws, fat, fecal samples, etc.; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL)
- Use mist nets
- Use (81H) Radio Transmitter (incl. nanotags) on White-throated Sparrow (WTSP) (5580)
  Lotek nanotag on up to 60 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Mark Black-throated Blue Warbler (BTBW) (6540) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Black-throated Blue Warbler (BTBW) (6540)
  Nanotag (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Mark Myrtle Warbler (MYWA) (6550) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Myrtle Warbler (MYWA) (6550)
  Lotek nanotag on up to 60 birds (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Mark Chestnut-sided Warbler (CSWA) (6590) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Chestnut-sided Warbler (CSWA) (6590)
  Nanotag (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Mark Blackpoll Warbler (BLPW) (6610) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Blackpoll Warbler (BLPW) (6610)
  Nanotag (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Mark American Redstart (AMRE) (6870) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on American Redstart (AMRE) (6870)
  Nanotag (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario

(continued on next page)

Environment Canada / Environnement Canada
Canadian Wildlife Service / Service canadien de la faune

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

Permit No.
N° de permis **10169 BU**

- Mark Swainson's Thrush (SWTH) (7580) with (01A) Plastic Colour Leg Band
  Single color band; RED WHI GRN BLUE BLACK in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Swainson's Thrush (SWTH) (7580)
  Nanotag (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario

See Permit Conditions on the following page -- Voir les conditions du permis sur la page suivante

(continued on next page)

Appendix 1c. Environment Canada, Canadian Wildlife Service scientific permit CA 0255. Issued to Christopher Guglielmo.

Environment and Climate Change Canada | Environnement et Changement climatique Canada

CANADIAN WILDLIFE SERVICE – PERMIT
PERMIS – SERVICE CANADIEN DE LA FAUNE

Permit to/for Permis de/pour	Permit no. No de permis
SCIENTIFIC	**CA 0255**

Organization Organization	Issued under section Délivré en vertu du paragraphe	Of De
Western University	**4(1)**	**MIGRATORY BIRD REGULATIONS**

Surname of holder Nom de famille du détenteur	Prénom du détenteur
Guglielmo	**Chris**

Dept. of Biology
1151 Richmond St. N
[redacted]

In accordance with section 19(1) of the Migratory Bird Regulations, th

- ☐ Kill a migratory bird
- ☑ Take a migratory bird, its nest or eggs
- ☐ Capture and band a migratory bird

Date of issue Date d'émission	Date of expiry Date d'expiration
May 2, 2017	**March 31, 2018**

By Signature	For Pour
[redacted]	[redacted]

Conditions – Conditions

1. Prior to any use of this permit the permittee will notify the Ontario Ministry of Natural Resources relative to collecting procedure s, times and localities of collection.
2. Landowner's permission must be obtained prior to collecting on private property.
3. Permit or a copy of the permit to be carried in the field by all collectors.
4. The permit holder is authorized to collect and to possess for scientific research purposes, read breath , blood, feather, claw, fat of White-throated Sparrow (Zonotrichia albicollis), Yellow-rumped Warbler (Setophaga coronata), Magnolia Warbler (Setophaga magnolia), Black-throated Blue Warbler (Setophaga caerulescens), from locations as situated within Oxford, Perth, Elgin, Middlesex, Norfolk, Haldimand, Essex, Kent, Bruce & Grey Counties within the province of Ontario.
5. Take is limited to a maximum of 100 specimens per species per year (except Zonotricia albicollis which is 400/year). The permittee is authorized to hold live birds for up to 14 days.
6. Capture, handling and sampling procedures are to be performed according to the Animal Care Committee protocols of the University of Western Ontario.
7. All other birds are to be released into the wild by the conclusion of the study or otherwise be humanely euthanized. No birds are to be donated or loaned to another individual or institution without the prior consent of the Canadian Wildlife Service.
8. Samples not to be retained are to be disposed of by the approved laboratory waste management system of the University of Western Ontario.
9. Permit holder shall submit a written report, by January 31, of each year following, indicating the results of the study to the Canadian Wildlife Service, 867 Lakeshore Road, Burlington, ON., L7R 4A6.
10. Nominees to this permit are: Department of Biology faculty/staff as acting under the direction of the permittee

Canada

Appendix 2. Banding data for spring 2017 for individuals included in analyses of migration timing, stopover duration, and/or refuelling rate. Trap type abbreviations: m = mist nets, g = ground traps. Sex and morph were determined genetically unless indicated by an asterisk.

Band number	Capture time (yyyy-mm-dd hr:min)	Trap type	Wing Chord (mm)	Age	Sex	Morph	Mass (g)	Fat mass (g)	Lean mass (g)	Harness size (mm)	Tag #
274169801	2017-04-16 9:00	m	73	s	m	w	25.3	2.56	20.85	NA	NA
274169802	2017-04-16 11:10	m	71	s	m	w	24.2	1.32	18.56	NA	NA
274169803	2017-04-16 11:50	m	73	a	m	t	25.5	0.96	21.04	NA	NA
274169804	2017-04-17 9:50	m	74	a	m	t	23.7	2.34	18.99	NA	NA
274169805	2017-04-18 7:05	m	71	s	m	w	23.6	2.27	17.89	NA	NA
274169806	2017-04-18 7:36	g	72	s	m	t	24.2	4.17	21.08	NA	NA
274169807	2017-04-18 8:20	g	75	a	m	t	23	2.59	20.66	NA	NA
274169808	2017-04-19 6:50	m	76	a	m	w	23.7	4.18	21.17	47	118
274169809	2017-04-19 9:50	g	76	a	m	w	24.4	1.92	21.2	NA	NA
274169811	2017-04-20 8:30	m	78	a	m	t	23.1	3.21	19.47	NA	NA
274169812	2017-04-20 8:30	m	72	s	m	w	22.9	1.94	19.83	NA	NA
274169816	2017-04-21 8:10	m	75	a	m	t	23.6	4.59	21.92	47	154
274169817	2017-04-21 8:20	m	76	s	m	w	23.7	2.05	20.76	NA	NA
274169818	2017-04-21 9:50	m	74	a	m	t	23.6	4.1	20.81	NA	NA
274169820	2017-04-22 8:10	m	72	s	m	t	23.9	3.14	19.96	NA	NA
274169821	2017-04-22 9:57	m	75	a	m	w	23.7	4.63	21.54	NA	NA
274169823	2017-04-22 11:42	m	74	s	m	w	24.4	3.14	20.43	NA	NA
274169825	2017-04-24 9:05	m	73	a	m	t	23.8	7.97	20.54	NA	NA
274169826	2017-04-24 10:43	m	72	s	m	w	24	4.99	20.01	NA	NA
274169828	2017-04-25 8:45	m	69	s	f	t	22.1	4.39	17.96	NA	NA
274169829	2017-04-25 9:30	m	69	a	m	w	23.3	6.61	20.37	45	112
274169830	2017-04-25 10:05	m	76	a	m	t	23.5	4.59	21.81	47	156
274169832	2017-04-26 8:20	m	72	s	m	t	24.4	4.81	20.13	NA	NA
274169833	2017-04-26 9:30	m	73	s	m	w	22.7	3.62	20.33	NA	NA
274169834	2017-04-26 9:50	m	74	a	m	t	23.4	5.1	19.1	46	157
274169835	2017-04-26 10:10	m	75	s	m	w	23.3	5.27	19.46	NA	NA
274169837	2017-04-26 11:00	m	70	s	m	w	23.7	3.37	19.39	NA	NA

274169838	2017-04-26 11:10	m	68	s	f	w	22.8	3.36	18.05	NA	NA
274169841	2017-04-27 7:50	m	74	a	m	w	24	NA	NA	NA	NA
274169843	2017-04-27 8:00	m	69	a	f	t	23.7	3.18	18.76	NA	NA
274169844	2017-04-27 8:00	m	68	a	f	t	22.9	1.33	16.07	45	116
274169846	2017-04-27 8:40	m	66	s	f	w	24.6	0.63	18.3	NA	NA
274169847	2017-04-27 8:50	m	72	a	m	w	24.4	2.85	19.25	NA	NA
274169848	2017-04-27 8:55	m	65	ahy	f	NA	NA	1.28	17.74	NA	NA
274169849	2017-04-27 9:10	m	69	s	f	t	24	3.94	18.54	NA	NA
274169850	2017-04-27 9:25	m	72	s	m	t	23.5	1.55	22.78	NA	NA
274169851	2017-04-27 10:50	m	69	a	f	t	23	3.15	18.83	NA	NA
274169852	2017-04-27 11:40	m	72	s	m	t	24.2	7.07	20.88	NA	NA
274169857	2017-04-28 8:45	m	68	s	f	w	24.3	0.36	18.23	NA	NA
274169858	2017-04-28 10:32	m	70	s	m	t	23.3	2.57	19.88	NA	NA
274169860	2017-04-28 10:50	m	68	s	f	w	21.9	2.2	18.09	NA	NA
274169862	2017-04-28 11:45	m	72	s	f	t	23.4	1.8	19.58	NA	NA
274169863	2017-04-28 11:45	m	71	s	f	t	23.2	0.71	18.53	NA	NA
274169864	2017-04-29 9:20	m	73	s	m	w	24.5	5.06	21.15	NA	NA
274169865	2017-04-29 10:30	m	66	a	f	t*	23.7	1.42	19.64	42	143
274169866	2017-04-29 11:30	m	70	s	f	t	22.8	2.74	19.07	NA	NA
274169868	2017-05-01 6:10	m	75	a	m	NA	24.75	4.51	19.05	NA	NA
274169869	2017-05-01 6:10	m	74	a	m	w	23.8	3.37	19.17	46	138
274169870	2017-05-01 6:10	m	67	a	f	w*	24.8	2.93	17.16	42	144
274169871	2017-05-01 7:40	m	73	s	m	t	24.1	3.1	18.98	NA	NA
274169872	2017-05-02 7:50	m	68	s	f	w	23.5	4.01	20.24	NA	NA
274169873	2017-05-03 7:10	m	74	a	f	w	23.8	3.18	19.27	46	137
274169874	2017-05-03 9:00	m	67	a	f*	t	22.3	3.13	18.6	42	147
274169875	2017-05-02 9:10	m	68	s	f	t	23.4	2.83	19.3	NA	NA
274169876	2017-05-03 10:50	m	72	s	m	t	24.4	6.09	20.42	NA	NA
274169877	2017-05-03 10:45	m	74	a	m	t	24.7	3.04	22.43	47	126
274169878	2017-05-03 11:50	m	76	s	m	w	23.7	2.94	19.71	NA	NA
274169881	2017-05-06 10:00	m	68	ahy	f	t	22.8	2.08	18.76	NA	NA
274169883	2017-05-06 11:00	m	68	s	f	w	23.42	5.45	19.55	NA	NA
274169884	2017-05-06 11:00	m	69	s	f	w	22.15	2.96	17.93	NA	NA
274169885	2017-05-07 8:15	m	74	s	m	t	24	5.24	21.54	NA	NA

274169886	2017-05-07 9:41	m	72	a	m	t	NA	4.35	19.45	NA	NA
274169887	2017-05-07 10:52	m	68	s	f	t	22.1	4.09	18.99	NA	NA
274169888	2017-05-08 8:50	m	64	s	f	t	22.8	2.81	17.35	NA	NA
274169889	2017-05-08 10:45	m	67	ahy	f	w	23	4.9	18	NA	NA
274169890	2017-05-08 11:30	m	72	s	f	t	21.3	NA	NA	NA	NA
274169891	2017-05-09 7:45	m	66	ahy	f	t	22.5	6.14	17.87	NA	NA
274169892	2017-05-09 8:16	m	72	a	f	w	23.3	3.56	17.45	NA	NA
274169893	2017-05-09 8:40	m	68	s	f	t	22	3.29	16.79	NA	NA
274169894	2017-05-09 9:30	m	69	ahy	f	w	24.2	2.63	20.05	NA	NA
274169895	2017-05-09 9:20	m	73	s	f	w	20.3	5.36	18.27	NA	NA
274169896	2017-05-09 9:45	m	67	a	f*	t*	22.6	7.03	18.7	43	161
274169898	2017-05-10 8:30	m	68	a	f*	t*	23.2	4.96	17.43	43	163
274169899	2017-05-10 8:30	m	69	a	f	t	NA	NA	NA	NA	NA
274169800	2017-05-10 9:25	m	70	s	f	w	23.12	6.56	19.24	NA	NA
277187301	2017-05-10 9:25	m	67	s	f	w	23.9	1.99	18.56	NA	NA
277187302	2017-05-10 10:40	m	74	a	m	w	24.8	6.64	21.62	NA	NA
277187303	2017-05-11 7:40	m	67	a	f*	t	24	3.19	18.27	43	164
277187304	2017-05-11 6:30	m	68	a	f	t	22.89	4.71	18.65	NA	NA
277187306	2017-05-11 9:30	m	67	a	f	t	23.6	5.2	19.67	NA	NA
277187307	2017-05-11 11:20	m	67	a	f	w	23.6	3.58	20.03	NA	NA
277187308	2017-05-12 7:37	m	70	s	f	w	23.7	3.55	17.31	NA	NA
277187309	2017-05-12 8:20	m	69	s	f	t	23.71	6.32	19.38	NA	NA
277187311	2017-05-12 8:40	m	69	s	f	w	23.3	6.87	19.2	NA	NA
277187312	2017-05-12 8:40	m	68	s	f	w	23.4	4.8	17.87	NA	NA
277187313	2017-05-12 9:40	m	66	s	f	t	NA	4.47	17.78	NA	NA
277187314	2017-05-12 10:00	m	72	s	f	w	21.56	7.68	18.76	NA	NA
277187315	2017-05-12 10:50	m	66	ahy	f	t	22.6	4.2	17.63	NA	NA
277187316	2017-05-12 11:00	m	68	a	f	t	22.14	2.84	19.72	NA	NA
277187324	2017-05-13 7:30	m	71	s	m	t	22.5	6.97	19.35	NA	NA
277187325	2017-05-13 8:00	m	69	s	f	w	22.7	4.65	17.89	NA	NA
277187326	2017-05-13 9:00	m	70	s	f	w	22.68	4.43	17.43	NA	NA
277187328	2017-05-13 9:35	m	71	s	f	w	22.9	3.28	17.82	NA	NA
277187329	2017-05-13 9:40	m	69	ahy	f	w	24.11	5.56	19.22	NA	NA
277187331	2017-05-13 10:30	m	68	ahy	f	NA	22.8	3.41	18.18	NA	NA

277187332	2017-05-14 7:40	m	68	s	f	t	23.5	4.1	18.02	NA	NA
277187333	2017-05-14 7:40	m	68	a	f	t	23.5	4.93	18.79	NA	NA
277187336	2017-05-14 8:42	m	69	s	f	w	23.5	6.04	18.43	NA	NA
277187337	2017-05-14 9:01	m	69	s	f	t	22.7	6.89	18.57	NA	NA
277187338	2017-05-14 9:30	m	68	ahy	f	t	23	5.72	20.83	NA	NA
277187339	2017-05-14 11:00	m	70	a	f	w	22.95	5.15	17.99	NA	NA
277187341	2017-05-15 9:10	m	66	s	f	w	22.9	6.11	18.56	NA	NA
277187342	2017-05-15 9:20	m	NA	a	m	t	NA	NA	NA	NA	NA
277187343	2017-05-16 8:03	m	66	s	f	t	20.9	3.61	17.05	NA	NA
277137261	2017-04-15 8:20	m	73	a	m	t*	22.5	2.47	18.56	47	110
277137266	2017-04-15 10:20	m	72	s	m	w	23.6	NA	NA	NA	NA
277137269	2017-04-16 6:30	m	76	a	m	w*	24.9	2.64	22.22	47	114
277137272	2017-04-16 7:20	m	73	a	m*	w	25.4	2.68	19.71	46	109
277137279	2017-04-16 9:10	m	75	a	m	w*	23.6	1.85	19.17	46	117
277137280	2017-04-16 8:20	m	72	a	m*	t*	23.5	4.35	18.85	45	108
277137292	2017-04-17 8:20	m	73	a	m	t	24.4	2.31	19.37	46	113
277138203	2017-04-18 8:50	m	74	a	m	t	24.3	3.27	19.47	46	153
277138206	2017-04-19 7:10	m	73	s	m	w	22.9	2.58	19.92	NA	NA
277138237	2017-04-21 9:50	m	74	a	m*	w*	24	2.78	18.7	46	120
277138245	2017-04-22 10:00	m	75	a	m*	w	23.3	3.35	20.34	46	121
277138255	2017-04-23 10:20	g	72	a	m	t	23.2	3.48	19.81	46	122
274169901	2017-04-23 8:20	m	74	s	m	w	23.3	2.65	18.37	NA	NA
274169908	2017-04-26 11:00	m	75	a	m*	t*	23.9	2.76	20.17	46	123
274169996	2017-04-27 9:20	m	68	a	f	w	23.7	4.25	17.8	45	130
277187056	2017-04-29 6:40	m	68	a	f*	w	23.8	0.98	19.58	44	128
277187055	2017-04-29 6:10	m	71	s	f	w	23.3	1.29	17.92	NA	NA
277187061	2017-04-29 7:00	m	67	a	f	w*	23.1	2.75	17.92	42	141
277187064	2017-04-29 7:30	m	67	a	f*	w*	23.8	3.76	18.15	42	140
277187068	2017-04-29 9:10	m	76	a	m	w*	24.3	2.44	20.01	46	124
277187095	2017-05-01 6:10	m	69	s	f	t	24.5	0.95	18.66	NA	NA
277187094	2017-05-01 6:10	m	67	a	f*	t	23.2	1.97	18.44	42	145
277187098	2017-05-01 6:40	m	68	a	f*	w	23.3	2.7	18.26	42	146
277187105	2017-05-01 7:50	m	71	a	m	NA	23.2	1.74	20.56	NA	NA
277187133	2017-05-02 7:10	m	67	s	f	w	23	3.68	19.32	NA	NA

277187136	2017-05-02 8:50	m	66	a	f	t*	23	2.02	18.66	41	150
277187148	2017-05-03 6:10	g	66	a	f	t	23	3.52	17.94	41	151
277187147	2017-05-03 7:00	g	66	a	f	w*	23.3	4.79	17.63	41	152
277187152	2017-05-03 6:50	m	65	s	f	t	21.4	0.96	16.44	NA	NA
277187156	2017-05-03 9:10	g	68	a	f	t	23.9	3.82	18.35	43	139
277187163	2017-05-06 6:10	m	68	a	f	t	22.8	2.38	17.33	NA	NA
277187165	2017-05-06 6:10	m	67	a	f	w*	25.42	3.59	17.71	43	142
277187164	2017-05-06 6:20	m	68	a	f	t	23.06	3.37	18.46	43	148
277187171	2017-05-07 6:00	m	72	a	m	w*	22.37	3.41	19.62	47	127
277187175	2017-05-07 6:00	m	67	a	f	t*	21.7	3.8	17.95	42	149
277187177	2017-05-07 6:00	g	75	a	m	t	23.89	5.13	20.93	46	111
277187176	2017-05-07 6:40	m	68	a	f	w*	23.4	4.75	19.29	44	132
277187184	2017-05-07 5:40	m	66	a	f	t	22.9	4.43	18.34	41	158
277187185	2017-05-07 6:00	m	68	s	f	w	23.4	7.33	20.47	NA	NA
277187197	2017-05-09 6:40	m	67	a	f	w	22.6	3.91	17.33	43	160
277187201	2017-05-09 6:40	m	74	a	m	w	22	5.15	20.56	45	133
277187210	2017-05-09 8:40	m	67	a	f*	w	23.1	3.37	18.65	42	159
277187226	2017-05-11 9:00	m	70	s	f	w	23.9	3.09	19.33	NA	NA
277187239	2017-05-11 9:30	m	69	ahy	f	NA	22.8	5.12	18.27	NA	NA
277187240	2017-05-11 9:30	m	68	ahy	f	NA	22	2.33	16.75	NA	NA
277187244	2017-05-11 9:40	m	68	a	f	w*	22.5	4.35	17.68	43	162
277187256	2017-05-12 10:20	m	71	a	f	t	23.2	6.2	19.85	45	134
277187269	2017-05-13 7:00	m	70	s	f	t	23.2	4.83	16.04	NA	NA
277187274	2017-05-13 7:00	g	63	s	f	w	21.3	4.19	14.9	NA	NA
277187279	2017-05-13 9:30	m	70	a	f	w*	22.8	5.7	18.66	45	135
277187284	2017-05-13 10:40	m	71	a	f	t*	25	7.97	21.03	45	136
277187291	2017-05-13 11:30	g	66	a	f*	t	22.5	3.92	16.67	43	155
277187293	2017-05-13 12:20	g	72	a	unk	w*	24	4.36	19.28	47	115

Appendix 3. Plasma metabolite concentrations from White-throated Sparrows sampled at the Long Point bird observatory during the spring of 2017.

Band number	Glycerol concentration ($mmol*L^{-1}$)	True triglyceride concentration ($mmol*L^{-1}$)	β-OH Butyrate concentration ($mmol*L^{-1}$)
274169801	0.56	1.368	1.7567365
274169802	0.54	0.929	0.617733
274169803	0.587	2.019	0.536571
274169804	0.607	1.277	1.8585805
274169805	0.619	2.142	0.189378
274169811	0.426	1.497	0.36086
274169812	0.414	1.527	0.7326385
274169817	0.642	1.282	0.895161
274169818	0.282	2.097	0.3196045
274169820	0.679	4.028	0.5544115
274169821	0.638	1.692	1.1285535
274169823	0.441	2.143	0.94057
274169825	0.414	2.062	0.175851
274169826	0.508	3.126	0.33694
274169828	0.532	2.424	0.63126
274169832	0.49	2.473	0.581287
274169833	0.375	3.174	0.589629
274169835	0.715	1.183	1.387407
274169837	0.454	2.339	0.19074
274169838	0.766	2.143	0.703404
274169841	0.508	1.706	1.427158
274169846	0.682	1.941	0.939425
274169847	0.465	1.24	1.378955
274169850	0.43	1.583	0.973944
274169851	0.499	2.167	0.34591
274169852	0.546	2.362	0.66584
274169857	0.39	1.282	0.4920285
274169858	0.247	1.606	0.604545
274169860	0.267	2.341	0.4836865

274169862	0.445	3.359	0.52531
274169864	0.624	1.677	0.68976
274169866	0.619	4.035	0.4665675
274169871	0.421	0.924	2.25652
274169872	0.307	2.888	0.496417
274169875	0.5	1.63	0.385941
274169876	0.226	3.46	0.38179
274169878	0.402	3.1	0.4469095
274169881	0.486	1.987	0.75853
274169883	0.674	4.093	0.536571
274169884	0.494	4.809	0.369112
274169885	0.528	2.328	1.282879
274169886	0.961	2.232	0.691473
274169887	0.351	3.198	0.467005
274169888	0.52	0.966	0.9815905
274169889	0.615	2.268	0.694447
274169890	0.921	7.432	0.4509
274169891	1.237	2.781	1.088925
274169892	0.695	1.452	1.3238995
274169893	0.957	1.081	1.173786
274169894	0.619	2.036	1.2813195
274169895	0.556	1.976	0.846735
274169800	0.666	1.77	0.910818
277187301	0.509	1.097	1.17115
277187302	0.823	2.376	0.7466385
277187304	0.666	2.486	0.6675715
277187306	0.579	1.137	1.319155
277187307	0.605	1.602	0.987265
277187308	0.79	1.413	1.257418
277187309	0.737	2.146	0.511208
277187311	0.497	1.85	0.78544
277187312	0.862	2.825	0.937596
277187313	0.626	2.443	0.4750545

277187314	0.691	2.482	0.661355
277187315	0.705	1.73	1.124455
277187316	0.343	3.153	0.39674
277187324	0.419	1.88	1.035105
277187325	0.697	2.423	1.229128
277187326	0.721	1.82	1.421355
277187328	0.574	1.381	1.02464
277187329	0.728	2.699	0.7524415
277187332	0.661	0.869	4.0650555
277187333	0.776	3.991	1.006161
277187336	0.522	4.41	0.64491
277187337	0.569	1.773	1.3655
277187338	0.356	3.532	0.631455
277187339	0.62	1.871	0.991492
277187341	0.556	2.123	0.9418395
277187343	0.547	1.977	0.739476

Cirriculum Vitae

Andrew Beauchamp

EDUCATION

Masters of Science in Biology (anticipated 2018) Western University, London, Ontario, Canada.

Bachelors of Science Biology (Honours) (2016) Trent University, Peterborough, Ontario, Canada.

AWARDS AND SCHOLARSHIPS

Trent National Renewable Scholarship, Trent University, September 2012 – April 2013, $1000.

Dean's Honour Roll, Trent University, September 2012 – April 2013.

Trent National Renewable Scholarship, Trent University, September 2013 – April 2014, $1000.

Dean's Honour Roll, Trent University, September 2013 – April 2014.

Trent National Renewable Scholarship, Trent University, September 2014 – April 2015, $1000.

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Trent National Renewable Scholarship, Trent University,September 2015 – April 2016, $1000.

Dean's Honour Roll, Trent University, September 2015 – April 2016.

President's Honour Roll, Trent University.

Ontario Graduate Scholarship, University of Western Ontario, September 2016 – August 2017, $15,000.

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Taverner Student Research Award, Society of Canadian Ornithologists, May 2018, $2,000.

CONTRIBUTIONS TO RESEARCH

Beauchamp, A.T., Y.E. Morbey, and C.G. Guglielmo. "Mechanisms underlying migration timing in the sexes and morphs of the White-throated Sparrow". Oral Presentation. Ontario Ecology, Ethology, and Evolution Colloquium. London, Ontario, Canada. May 2018.

Beauchamp, A. T., Y. E. Morbey, and C.G. Guglielmo. "Mechanisms underlying migration timing in the sexes and morphs of the White-throated Sparrow". Oral Presentation. 27th Annual Comparative Physiology and Biochemistry Workshop. Keene, Ontario, Canada. January 2018.

Beauchamp, A.T., Y.E. Morbey, and C.G. Guglielmo. "Mechanisms underlying migratory protandry in the sexes and plumage morphs of the White-throated Sparrow". Poster presentation. Biology graduate research forum, London, Ontario, Canada, 2017.

Beauchamp, A.T., Y.E. Morbey, and C.G. Guglielmo. "Mechanisms underlying migratory protandry in the sexes and plumage morphs of the White-throated Sparrow". Poster presentation. AOS-SCO conference 2017. East Lansing, Michigan, USA, 2017.

Beauchamp, A.T., Y.E. Morbey, and C.G. Guglielmo. "Mechanisms underlying migration timing in the sexes and morphs of the White-throated Sparrow". Poster Presentation. 26th Annual Comparative Physiology and Biochemistry Workshop. Keene, Ontario, Canada. January 2017.

EMPLOYMENT

Teaching assistant, Wildlife Ecology and Management, Western University, January 2018 – April 2018.

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Research assistant, Trent University, Peterborough, Ontario, Canada, May – August 2015.

PUBLICATIONS

Morbey, Y.E., and A.T. Beauchamp (In review). Evidence of preparatory behaviour on migratory departure days in free-living songbirds. Biology letters.